THE ANTERIOR COMMISSURE OF THE RABBIT

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A DESCRIPTIVE AND EXPERIMENTAL ANATOMICAL STUDY WITH AN ATLAS OF THE RABBIT' TELENCEPHALON IN HORIZONTAL SECTIONS

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR IN DE GENEESKUNDE
AAN DE KATHOLIEKE UNIVERSITEIT TE NIJMEGEN OP GEZAG
VAN DE RECTOR MAGNIFICUS MR. S. F. L. BARON VAN WIJNBERGEN,
HOOGLERAAR IN DE FACULTEITEN DER RECHTSGELEERDHEID
EN DER SOCIALE WETENSCHAPPEN,
VOLGENS BESLUIT VAN DE SENAAT
IN HET OPENBAAR TE VERDEDIGEN OP MAANDAG 23 JUNI 1969,
DES NAMIDDAGS TE 4 UUR

door

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geboren te Venlo

1969

H. J. W. BECHT'S UITGEVERSMAATSCHAPPIJ N.V., AMSTERDAM

Dit proefschrift werd bewerkt in het laboratorium voor anatomie en embryologie (hoofd Prof Dr H J Lammers) van de Katholieke Universiteit te Nijmegen onder supervisie van Dr A H M Lohman

Het proefschrift verschijnt tevens als supplement 57 — 1 ad Vol 74 (1969) van de 'Acta Anatomica'

Voor Vader en Moeder

CONTENTS

The present paper is an account of the origin, course and distribution of the nerve fibres of the posterior limb and the stria terminalis component of the anterior commissure, as observed during an experimental neuro anatomical study in the rabbit

As early as 1879, Sigbert Ganser defined the problem with regard to the anterior commissure as follows 'Es gilt in erster Linie festzustellen, in welchen Rindenbezirken die vordere Commissur endigt, in zweiter Linie, was für Fasern dieselbe führt, ob gekreuzte oder Commissurfasern oder beides' Since then, many investigators have included the anterior commissure in their studies of the basal telencephalon In the past few decades detailed information about the anterior limb of this commissure has been obtained with silver impregnation methods demonstrating degenerating axons It is peculiar, however, that the posterior limb and the stria terminalis component have only been described incidentally and incompletely Since Ganser's study in which the atrophy method was made use of, only a few studies have been particularly concerned with the anterior commissure Kreiner (1936) presented a myelo architectonic and topographical description of the commissure in the rat Bailey, Garol and McCulloch (1941), McCulloch and Garol (1941), and Garol (1942) studied the origin of the fibres in the anterior commissure in monkeys and cats by electrophysiological methods After local strychninization of one hemisphere, these authors examined the electrical activity of both hemispheres before and after dividing the corpus callosum Fox (1943), Fox and Schmitz (1943) and Fox, Fisher and Desalva (1948) made use of the Marchi method in their study of the anterior commissure of cats and monkeys Brodal (1948) investigated the distribution of the retrograde cellular changes after section of the anterior commissure in rats However after studying the relevant literature it appears that the present state of knowledge, particularly pertaining to the posterior limb and the stria terminalis component of the anterior commissure, has advanced little beyond that of a hundred years ago, and that the questions posed by Ganser still remain to be answered

From previous reports, it appears that the fibres of the anterior commissure after decussating the midline of the brain can only be followed over a short distance in the hemisphere In several instances fibres have been described ending in defined cortical or subcortical areas Such fibres form only a small portion of the total number of fibres which is suggestive that the anterior commissure has a very diffuse distribution This, however, cannot be demonstrated in normal material, nor with the aid of non selective degeneration methods Neither has a final answer to these problems been obtained by the use of the Marchi method, a technique that contributed greatly to the evolution of neuroanatomical research in the first few decades of this century Although this method permits the possibility of selective staining of degenerating myelin sheaths (see e g Strich, 1968), interpretation of the results is often difficult because of the frequent occurrence of artefacts Furthermore, the termination of the fibres cannot be demonstrated by this method For these reasons, methods of silver impregnation are usually preferred nowadays, especially in studying diffuse neural connections For reviews of these methods see Evans and Hamlyn (1956), Bowsher, Brodal and Walberg (1960) and Heimer (1967, 1968, 1969)

In the present study the methods used are the Nauta Laidlaw method (Nauta, 1957), Jacobson's modification of Nauta's method (Jacobson, 1963), and the method of Fink and Heimer (1967) Use was also made of the combined cell and myelin stain of Kluver and Barrera (1953)

In earlier studies of the anterior commissure, almost exclusive use was made of transverse sections through the brain During the present investigation it became obvious that the maximal spread of fibres of the commissure is in the horizontal plane Therefore, most brains were cut horizontally This necessitated the use of a topographical atlas of the rabbit telencephalon based on horizontal sections Since information of this nature was not available in the literature, description of the experimental results is preceded by such an atlas (part I) In addition, a number of transverse sections has been reproduced for better orientation In general, the nomenclature used is that proposed by Rose (1931), and Young (1936) However, at controversial points, the personal view of the author is submitted

As starting point for the experimental study of the anterior commissure lesions were made in the midline of the commissure, from which it might be expected that symmetrical degeneration of fibres in both hemispheres would occur The lesions had to be as small as possible to prevent damage to adjacent structures which would make it difficult to evaluate the results The best method for this purpose was coagulation with a fine electrode An alternative

to reduce confusion due to degenerating fibres from adjacent structures was to make lesions at different sites along the course of the fibres of the anterior commissure In addition, this permitted verification of the findings obtained in the first group of experiments From all these studies, data could only be obtained about the efferent fibres of the anterior commissure Consequently, to study the origin of the fibres lesions were made in different cortical and subcortical areas These experiments and the results obtained will be discussed in part II of the present study

Part I

SURVEY OF THE STRUCTURE OF THE RABBIT TELENCEPHALON

INTRODUCTION

In the last decades descriptive studies of animal brains have gradually diminished in favour of experimental techniques. However, exact documentation of topography is still essential since it constitutes an indispensable aid both for the correct localization of lesions, and the interpretation of the results obtained. Already in the early stages of experimental neuro-anatomical research on the brains of laboratory animals, various atlases were prepared to satisfy this need. Of these, the atlas of Winkler and Potter (1911) is still invaluable for the study of the rabbit's brain. Details of the cerebral cortex of the rabbit are given in the cyto-architectonic study of Rose (1931), and a systematic description of the subcortical structures can be found in Young's work (1936). The comparative anatomical studies of Winkler (1917), Ariëns Kappers, Huber and Crosby (1936) and Crosby and Humphrey (1939, 1941) are also of great merit. All these investigations are based on transverse sections of the brain. In the present study of the anterior commissure most brains were cut in the horizontal plane. For purposes of reference drawings had to be prepared from representative horizontal sections through the entire rabbit telencephalon. In these illustrations attempts have been made to present the topography of various cortical and subcortical structures without giving excessive cyto-architectonic detail. A number of drawings of transverse sections are also given.

The labelling of the various structures was complicated by the confused nomenclature generally applied to the telencephalon. This is probably due to the many problems which still have to be solved about the phylogeny and ontogeny of the telencephalon. Furthermore, several authors have rather inaccurately introduced into neuro-histology terms derived from macroscopical neuro-anatomical literature. In the present study it has been impossible to reconcile these diverse arguments. The nomenclature finally adopted should

be regarded as provisional, we have listed the considerations which led us to choose particular terms

MATERIAL AND METHODS

For the analysis of the structural relations in the telencephalon, three male New Zealand rabbits were used (aged 4 months, body weights between 2000 and 2500 g) Under Nembutal anaesthesia (30 mg per kg body weight, i v), the animals were perfused with physiological saline (40 ml per kg body weight) and 10% formol saline (100 ml per kg body weight) After 12 to 24 hours the brains were removed and stored in 10% formalin for at least 3 weeks The brains were subsequently embedded in paraffin and cut in serial sections 15 μ thick in the horizontal plane (two brains) and in the transverse plane (one brain) Every 10th section was stained by the combined cell and myelin stain of Kluver and Barrera (1953)

From the two horizontal series, 16 representative sections were selected and drawn In addition, from the same sections microphotographs were prepared (pages 32–63) From the transverse series, 6 sections were drawn (pages 64–67) The drawings are labelled with the serial numbers of the corresponding sections (from dorsal to ventral and from rostral to caudal, respectively), so that the distances between the different sections can be calculated

The magnification of the horizontal sections Nos 140–520 and of the transverse sections is approximately 10× The horizontal sections Nos 560–830 have been magnified 15×

CLASSIFICATION AND NOMENCLATURE

Topographical descriptions of the telencephalon of the rabbit may be based on its macroscopic subdivision into a pars dorsalis and a pars ventralis (for a schematic drawing see page 30) The border line between these two areas at the lateral side of the hemisphere is the fissura rhinalis On the medial side, there is a transitional area between these two parts which is formed by the cingulate gyrus We will consider to what extent this division correlates with existing classifications of the telencephalon, and on which criteria the various terms used in the literature are based

Classifications of the telencephalic cortex are mostly based on cyto-architectonic, myelo-architectonic or ontogenetic differences between the various cortical areas. For instance, the distinction made by Brodmann (1909) between 'homogenetische und heterogenetische Formationen' is based on differences between the lamination of the two cortical areas in a particular stage of the embryonal development. Allegedly, the homogenetic cortex has a basic structure of six layers which cannot be demonstrated in the heterogenetic cortex. Therefore, the latter has a more primitive structure. It can be further subdivided into a cortex primitivus, a cortex rudimentarius and a cortex striatus. The homogenetic cortex defined by Brodmann consists of the above-mentioned pars dorsalis of the telencephalon and the cingulate gyrus, while the heterogenetic cortex corresponds to the cortex of the pars ventralis.

Vogt and Vogt (1920) pointed out myelo-architectonic differences between the two cortical areas of Brodmann, and, in view of these differences, introduced the terms 'isocortex' and 'allocortex'. According to these authors, the isocortex is characterized by the termination of the radial fibrous plexus in the third layer, whereas in the allocortex these fibres terminate in the superficial layer. Subsequently, Lorente de Nó (1933, 1934) called the attention to the relatively small number of cells with short axons, the so-called Golgi type II cells, in the allocortex.

Rose (1926, 1927, 1931) distinguished three types of cortex on the basis of ontogenetic criteria: the cortex totoparietinus (totocortex) the cortex semiparietinus (semicortex) and the cortex bigenitus (bicortex). According to Rose, in the totocortex all the cells of the wall of the secondary brain vesicle are involved in the formation of the cortex. In the semicortex only part of these cells participate in forming the cortex, while the majority are used in the development of the corpus striatum. Rose includes in the semicortex: the regio praepyriformis, the regio periamygdalaris, the tuberculum olfactorium, the septum pellucidum and the area diagonalis. The other cortical areas are part of the totocortex, with the exception of a transitional area between the semicortex and the totocortex around the fissura rhinalis, which he called cortex bigenitus. Rose's further subdivision is based on the degree of differentiation of the various cortical areas in subsequent ontogenetic development. From this it appears that only the cortex corresponding to the above-mentioned pars dorsalis differentiates to a structure with seven layers. In this stage of embryonic development, Rose's classification is in accordance with Brodmann's distinction between homogenetic and heterogenetic areas.

Differences in the phylogenetic development of the telencephalic cortex has also led to a subdivision of the cerebral cortex. Ariens Kappers (1929) dist-

inguished three cortical areas which in his opinion develop sequentially during phylogenetic development the palaeocortex, the archicortex and the neocortex (the terms 'archicortex' and 'neocortex' had already been introduced by Elliot Smith, 1901) In this respect, the relation between the various cortical regions and the olfactory bulb is of predominant importance According to Ariens Kappers, the palaeocortex receives secondary olfactory fibres exclusively, whereas the archicortex is mainly a tertiary olfactory area The neocortex, however, is not believed to receive olfactory fibres but receives fibres from the neothalamus From the level of the lowest mammals it appears that the palaeo cortex (prepiriform and piriform cortex) and the archicortex (hippocampal cortex) have a fairly constant organization In subsequent differentiation of the telencephalon, the topography is influenced by progressive development of the neocortex Owing to this neocortical proliferation between the palaeocortex and the archicortex, the latter two structures are displaced in ventral and medial directions, respectively, and along the border line between the neo cortex and the palaeocortex the rhinal fissure is formed

In the descriptive anatomical and in the neurophysiological literature, it was the anatomy on the medial side of the hemisphere that first gave rise to confusion By naked eye inspection Broca (1878) noted in man that the cortex of the medial wall of the hemisphere and the mediobasally situated structures of the telencephalon are continuous with each other These areas, which are grouped as a girdle around the hilus of the hemisphere, were called by him the 'grand lobe limbique' The term 'lobus limbicus' or 'area limbica' is still used in the literature, although with many different meanings (cf Rose, 1926, Papez, 1937, Rose and Woolsey, 1948) It was MacLean (1952) who ultimately defined the 'limbic cortex' as the cortex which has close reciprocal connections with the hypothalamus The functional relationship between the limbic cortex and the brain stem areas connected with it has been expressed in the term 'limbic system', an equivalent of the term 'visceral brain', which is used particularly in the neurophysiological literature The concepts and terminology proposed by MacLean have been employed by many other investi gators (e g Nauta, 1956, 1958) Precise anatomical analysis of the limbic lobe as originally defined by Broca has shown that this area consists of three highly different structures, viz the subcallosal gyrus, the cingulate gyrus and the parahippocampal gyrus Of these the parahippocampal gyrus, which is part of the palaeocortex according to Ariens Kappers, Huber and Crosby (1936), is now regarded by most investigators as part of the piriform lobe (Gastaut and Lammers, 1961) The cingulate gyrus has been described (e g by Papez, 1937) as a component of the limbic cortex, because of its connections with the hippo

campus. However, cyto architectonic studies by Rose (1926) and Filimonoff (1929, 1947) showed that this area has the structure of transitional cortex (mesocortex, peri-archicortex). According to Rose it has differentiated much farther in ontogenesis than the ventral cortical areas, so that it shows more resemblance to the neocortex situated dorsal to it. Recent experiments by Domesick (1969) have shown that 'the subcortical projections of the cingulate cortex resemble those of the isocortex more than they do those of the limbic telencephalon.' Accordingly, on the basis of these findings, the cingulate gyrus has not been accepted as part of the limbic lobe in the classification presented below, but has been put as a medial transition zone between the dorsal and ventral portions of the telencephalon.

In the literature the term 'rhinencephalon' is also used with many different meanings (Bargmann and Schadé, 1963), but mostly it is used to indicate the allocortical complex of the olfactory lobe and the limbic lobe (Gastaut and Lammers, 1961). Since this term, like 'olfactory brain,' refers to a function which is not represented equally in all the corresponding structures, nowadays more topographically accurate terms are preferred.

For the description of the various areas of the telencephalic cortex, the nomenclature of Rose (1931) is used almost without exception in the modern literature. On the basis of the above-mentioned cyto-architectonic criteria, this author has subdivided the cerebral cortex of the rabbit into 24 regions which correspond approximately to the topographic units encountered in the telencephalon. For this reason, Rose's nomenclature has been made use of in the present study.

Details of the phylogenetic and ontogenetic development of the various subcortical structures will not be discussed These are given by Kuhlenbeck (1924), Ariens Kappers (1929) and Ariens Kappers, Huber and Crosby (1936). The nuclear areas have been described by Young (1936) and the nomenclature of this investigator will also be used here.

On this basis the following classification can be made

Topographical subdivision of the telencephalon of the rabbit

A. Pars Dorsalis Telencephali
   1. Regio Praecentralis Agranularis
   2. Regio Praecentralis Granularis
   3. Regio Postcentralis
   4. Regio Parietalis
   5. Regio Temporalis
   6. Regio Occipitalis with Area Striata

B. Lateral Transition Zone
    1. Regio Insularis Agranularis et Regio Insularis Granularis
    2. Regio Perirhinalis

C. Pars Ventralis Telencephali
  I. Lobus Olfactorius
    a. Lobus Olfactorius Anterior
      1. Bulbus Olfactorius
         Bulbus Olfactorius Accessorius
      2. Area Retrobulbaris
      3. Regio Praepiriformis
      4. Tuberculum Olfactorium
      5. Area Diagonalis
    b. Lobus Olfactorius Posterior or Lobus Piriformis
      1. Amygdala
      2. Gyrus Parahippocampi
           Regio Entorhinalis
           Parasubiculum
           Praesubiculum
  II. Basal Ganglia
      1. Putamen
      2. Globus Pallidus
      3. Nucleus Caudatus
      4. Nucleus Accumbens
      5. Claustrum
  III. Lobus Limbicus
    a. Area Septalis
    b. Limbus Hippocampi
      1. Pars Praecommissuralis or Anterior Continuation of the Hippocampus
      2. Pars Supracommissuralis or Indusium Griseum
      3. Pars Retrocommissuralis or Formatio Hippocampi
           Subiculum
           Gyrus Hippocampi
           Gyrus Dentatus

D. Medial Transition Zone
    Gyrus Cinguli
      1. Regio Infraradiata
      2. Regio Retrosplenialis

The prepiriform region

Although a detailed description of the various areas of the telencephalon is beyond the scope of the present study, an exception has been made for the prepiriform cortex. In the literature, this term has not always been used to indicate the same cortical area.

The prepiriform cortex derives its name from the piriform lobe which is a macroscopically visible structure occupying the ventrolateral portion of the telencephalon (see figures on page 30). On the rostral side, the piriform lobe (posterior olfactory lobe) is sharply delimited from the anterior olfactory lobe by the incisura olfactoria (Gastaut and Lammers, 1961). On this basis the term 'prepiriform cortex' should *sensu stricto* mean only the cortical area on the ventrolateral side of the anterior olfactory lobe, which extends from the olfactory bulb to the incisura olfactoria. In that case, the term 'piriform cortex' would apply to the entire cortex of the piriform lobe, including the entorhinal cortex, the parasubiculum and the praesubiculum. It is curious to note that no one in the literature has employed these two terms in the sense described above.

Ariëns Kappers, Huber and Crosby (1936) used the term 'piriform lobe cortex' to indicate the entire cortical area on the ventrolateral side of the olfactory lobe, extending from the olfactory bulb rostrally to the hippocampal area caudally. Thus defined, the piriform lobe cortex represents the palaeocortex in the above-mentioned phylogenetic classification of Ariëns Kappers. However, in that case, the term 'lobus piriformis' no longer has the meaning given above, but now also includes part of the anterior olfactory lobe.

Cyto-architectonic and myelo-architectonic studies have not shown any structural differences between the cortex on the ventrolateral side of the anterior olfactory lobe and the rostral portion of the cortex of the piriform lobe. Consequently Rose (1931) called this entire area the 'regio praepyriformis', which corresponds to area 51 of Brodmann (1909). At the site of the caudal end of the amygdaloid complex, the 'regio praepyriformis' passes into the regio entorhinalis (area 28 of Brodmann), which can clearly be distinguished cyto-architectonically from the regio praepyriformis. The terminology of Rose has been utilized by a number of authors (e.g. Stephan, 1963; Scalia, 1966). Other investigators have agreed with the boundaries of the regio praepyriformis as described by Rose, but call it 'piriform cortex' (Young, 1936; Brodal, 1947; Knook, 1965). An objection to the last-mentioned term is that it results in extension of the original term 'piriform cortex' to include the cortex of the anterior olfactory lobe, while the caudal portion of the cortex of the piriform lobe is given a different name: 'entorhinal cortex'.

The term 'piriform cortex' is interpreted by Gray (1924), in agreement with

Ariëns Kappers and others, to mean the entire cortical area on the ventrolateral side of the olfactory lobe, which Gray subdivides into a pars anterior, a pars medialis and a pars posterior. The distinction between the pars medialis and the pars posterior is based on cyto-architectonic differences between these two areas, while the incisura olfactoria constitutes the border line between the pars anterior and the pars medialis. In other words, this latter distinction is based on a macroscopical criterion and ignores the cyto-architectonic identity of these two areas. Certain investigators (e.g. Valverde, 1963) call the areas distinguished by Gray the 'area praepiriformis', 'area piriformis', and the 'area entorhinalis', respectively. Since Gray used the term 'piriform cortex' for the entire cortical area, Sanders-Woudstra (1961) used the term 'area periamygdaloidea' for the pars medialis, and her example was followed by Lohman (1963) and Lohman and Lammers (1963). However, the last-mentioned term leads to confusion, since Rose (1931) reserved the term 'regio periamygdalaris' for the superficial structures of the amygdaloid complex and the cortex surrounding this complex.

From the hodological point of view also, there are similarities between the cortex on the ventrolateral side of the anterior olfactory lobe and the rostral portion of the cortex of the piriform lobe. It has been demonstrated experimentally that this entire area, which corresponds to Rose's prepiriform region, can be regarded as a secondary olfactory projection area (Le Gros Clark and Meyer, 1947; Sanders-Woudstra, 1961; Lohman, 1963; Lohman and Lammers, 1963). In addition, distinct differences have not been found between these two cortical areas when considering their hodological connections with the posterior limb of the anterior commissure (see part II of the present study).

For these reasons, we consider that the term 'prepiriform region' should be used for the cortical area on the ventrolateral side of the telencephalon, which extends from the olfactory bulb rostrally to the entorhinal region caudally. The dorsolateral boundary of this cortex is the fissura rhinalis, where the prepiriform region passes into the neocortex via the insular region. On the medial side, the prepiriform region is delimited rostrally by the olfactory tubercle and caudally by the amygdaloid complex. It is separated from these areas by the fissura endorhinalis. Even when defined in this manner, the term 'prepiriform region' is not particularly appropriate because in the rabbit and a few other macrosmatic animals the prepiriform cortex extends over part of the surface of the piriform lobe. However, this nomenclature does justice to this entire cortex as a histological unit.

The boundaries between the prepiriform region and the adjacent structures on the dorsolateral and caudal sides are easy to define. The same holds true

for the demarcation between this region and the olfactory tubercle On the other hand, the prepiriform region passes rostrally into the retrobulbar area without a distinct boundary The retrobulbar region has been described by Herrick (1924) in the opossum as an 'undifferentiated portion of the secondary olfactory area', to which he gave the name 'anterior olfactory nucleus' Other investigators adopted this term, but, unlike Herrick, they regarded the anterior olfactory nucleus as a separate nuclear area On the basis of differences in cell size and organization it has been subdivided into six parts (Lohman, 1963, for the guinea pig, Lohman and Mentink, 1969, for the rabbit) There are, however, clear cyto architectonic and hodological resemblances between the so-called pars lateralis of the anterior olfactory nucleus and the prepiriform region situated caudal to it, which suggests that the pars lateralis of the anterior olfactory nucleus should be regarded as a rostral continuation of the prepiriform cortex, as originally was described by Herrick There is a similar relationship between the superficial cell layer of the so-called pars medialis of the anterior olfactory nucleus and the anterior continuation of the hippocampus (Rose's taenia tecta) Accordingly, we agree with Nieuwenhuys (1967) that too strict a separation of the area immediately caudal to the olfactory bulb from the telencephalic areas situated farther caudally is not justified, and that the neutral term 'retrobulbar area' is to be preferred for this region

There are different opinions in the literature about the medial border of that part of the prepiriform region which is situated caudally to the olfactory tubercle Ariens Kappers, Huber and Crosby (1936) state that the medial border of the piriform lobe cortex is the fissura endorhinalis et amygdalae According to them, this fissure is formed during phylogenetic development of the telencephalon because the palaeocortex is forced against the structure situated medially to it (the olfactory tubercle and the amygdala) Rose, however, described the medial border of the prepiriform region as lying at some distance lateral to the endorhinal fissure The cortical area in between, which he called 'area periamygdalaris lateralis' (Pam I), is regarded as part of the regio periamygdalaris which forms the cortex superficial to the amygdala Cyto architectonic studies have shown that Rose's area 'Pam I' has a distinct resemblance to the 'area praepyriformis intermedia' situated lateral to it Other investigators have not always distinguished clearly between the prepiriform region and the amygdaloid complex, but from their descriptions it can be deduced that the border line between these two regions lies at the endorhinal fissure (Brodmann, 1909, Johnston, 1923, Crosby and Humphrey, 1941, Brown, 1967) The experimental investigation described in the second part of the present study has revealed that in cases in which there is terminal degeneration in the

prepiriform cortex, the degeneration proceeds in a ventromedial direction up to the endorhinal fissure Accordingly, the present investigator regards this fissure as the mediocaudal limit of the prepiriform region Like Crosby and Humphrey (1941), the term 'cortico-amygdaloid transition area' is here used for the transition area which lies medial to the endorhinal fissure between the prepiriform cortex and the cortical amygdaloid nucleus The same term has been applied to the transitional zone between the cortical amygdaloid nucleus and the entorhinal cortex caudal to it

The anterior commissure

At low power magnification the anterior commissure can be seen as a thick, almost round bundle of myelinated fibres, which crosses the lamina terminalis just rostral to the 3rd ventricle and the columns of the fornices In the commissure a number of components can be distinguished Most of the early investigators mentioned only two components the pars olfactoria and the pars temporalis (Ganser, 1879, Winkler and Potter, 1911, 1914) A contribution from the stria terminalis was described by Johnston (1923) and Berkelbach van der Sprenkel (1926) in the opossum and by Gurdjian (1925) in the rat Young (1936) distinguished in the rabbit an anterior limb, a transverse and a posterior limb of the anterior commissure He also described a commissural component of the stria terminalis Humphrey (1936) demonstrated eight components in the bat After trying to compare her findings with those of other investigators, she concluded that 'it has not been possible to homologise precisely the components described by these observers with those found in the bat'

In more recent literature, three components are usually being distinguished in the anterior commissure (Ariens Kappers, Huber and Crosby, 1936, Kreiner, 1936, Fox and Schmitz, 1943, Lohman, 1963)

1. crus anterius sive pars olfactoria
2 crus posterius sive pars interhemispherica
3 pars ad striam terminalem

This classification is mainly based on topographical and myelo-architectonic studies of normal material For the present, it does not seem useful to make further subdivisions, especially of the posterior limb, as long as experiments have not yielded exact data about the fibre distribution of this component

In the midline of the brain the thickly myelinated fibres of the anterior limb occupy the rostroventral portion of the anterior commissure The fibres of the other two components are more thinly myelinated and are difficult to distinguish from one another.

On each side of the brain the anterior limb passes rostral to the column of the fornix as a compact bundle and then curves in a rostroventral direction toward the olfactory peduncle. Via two large projections the fibres of this component of the anterior commissure constitute a non-commissural connection between the olfactory bulb of one hemisphere and the retrobulbar area of the other hemisphere. The anterior limb does not receive any fibres from other regions of the basal telencephalon (Lohman, 1963; Lohman and Lammers, 1961, 1963). The posterior limb curves first ventrorostrad and then runs in a lateral direction where it is surrounded for most of its course by the anterior ventral portion of the putamen. Having reached the lateral position the bundle ends in a caudally-directed fibre radiation which fans out in the external capsule. Throughout the course of the posterior limb separate small bundles split off. These run a curved course in a rostrolateral direction and are intertwined with fibre bundles of the internal capsule. A number of these bundles run parallel to the lateral side of the anterior limb over a considerable distance, so that they seem to be part of it. All the small bundles fan out in the most rostral portion of the external capsule. This latter component was first described by Young (1936) in the rabbit as the transverse limb of the anterior commissure. Kreiner (1936) described this component in the white rat as follows: 'Diese Fasernbündel kommen bei der Ratte bei allen Individuen vor, auch wurden sie bei anderen Tieren beobachtet. In das Striatumgebiet kommen sie latero-ventral vom Hauptbündel (Pars Olfactoria) durch die Capsula externa, von dem im unteren Teile dieser letzteren aus dem Pedunculus olfactorius verlaufenden Bündel. Wir wollen sie als überzählige Bündel der Commissur (Fasciculi accessorii partis olfactoriae commissurae anterioris) bezeichnen.' In the rabbit, where this part of the anterior commissure stands out more clearly than in other commonly used laboratory animals (rat, guinea-pig, etc.), the topographical relationship with the posterior limb is clearly displayed. The fibres in these fasciculi are also more thinly myelinated than those of the anterior limb. We consider therefore, unlike Kreiner, that this 'pars transversa' should be regarded as a component of the posterior limb of the anterior commissure.

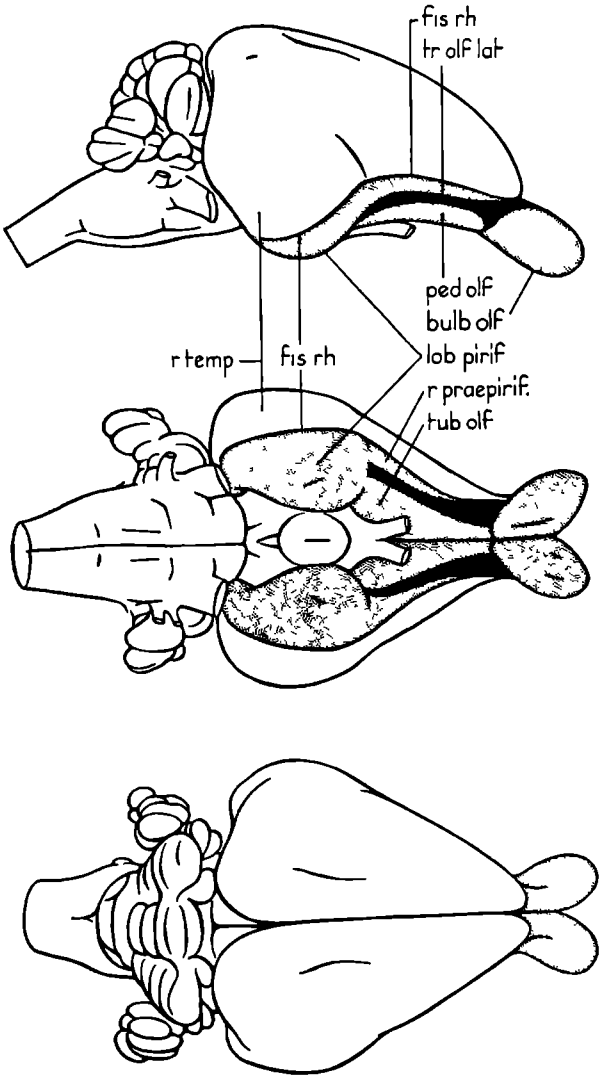
The pars ad striam terminalem is the smallest component of the anterior commissure and occupies its dorsocaudal part. Immediately after crossing the midline it leaves the commissure in a dorsocaudal direction and runs with the other components of the stria terminalis on the medial side of the internal capsule. At its most dorsal level, the stria terminalis lies in the sulcus between the caudate nucleus and the thalamus (sulcus terminalis). Subsequently, the bundle lies medial to the tail of the caudate nucleus and curves in a ventral and

rostral direction finally reaching the amygdaloid complex, where it is found alongside the lateral wall of the lateral ventricle. At the level of the central amygdaloid nucleus the commissural component again separates from the rest of the stria terminalis and runs rostrad to the nucleus of the lateral olfactory tract. The fibres of this commissural component do not intermingle with the other fibres of the stria terminalis, and, because of their thicker myelin sheaths, they can clearly be distinguished as a separate bundle throughout their entire course.

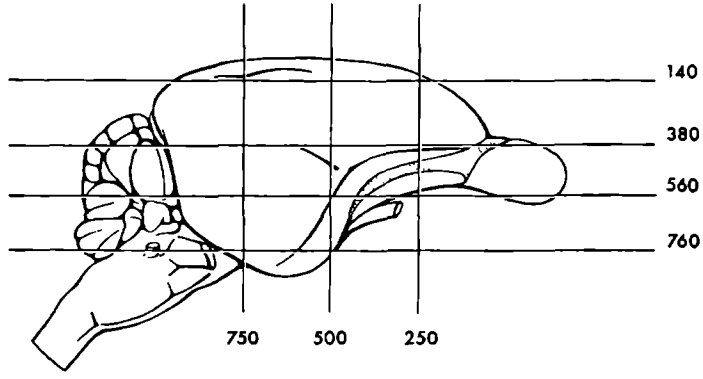
ATLAS

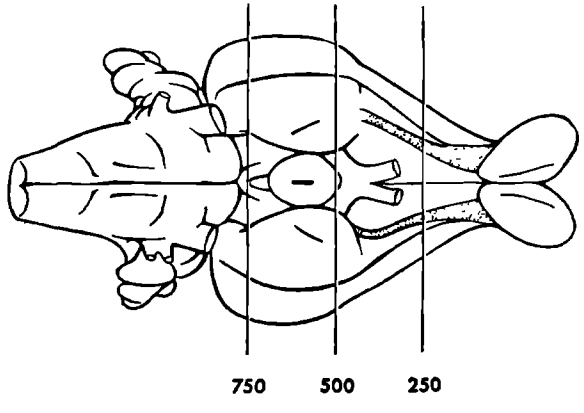
a. am. ant.	area amygdaloidea anterior
ant con. hip.	anterior continuation of the hippocampus
a. praeop.	area praeoptica
a. retrob.	area retrobulbaris
a. str.	area striata
b. olf.	bulbus olfactorius
b. olf. acc.	bulbus olfactorius accessorius
c. a. c. ant.	commissura anterior, crus anterius
c a. c. post.	commissura anterior, crus posterius
c. a. p. tr.	commissura anterior, pars transversa
c. c.	corpus callosum
c. c. f ant	corpus callosum, forceps anterior
c. c. f. post.	corpus callosum, forceps posterior
c. ext.	capsula externa
c. int.	capsula interna
ch. op.	chiasma opticum
cing. b.	cingulum bundle
cl.	claustrum
col fx	columna fornicis
comm. fx	commissura fornicis
comm. hip.	commissura hippocampi
cort. am. tr a.	cortico-amygdaloid transition area
fi. hip	fimbria hippocampi
fis. end.	fissura endorhinalis
fis. rh.	fissura rhinalis
fx	fornix
g. dent.	gyrus dentatus
g. hip.	gyrus hippocampi
gl. pall.	globus pallidus
hyp.	hypothalamus
ind. gr.	indusium griseum
ins. C.	insula granularis of Calleja
ins. med. C.	insula granularis medialis of Calleja
m. f b.	medial forebrain bundle
n. acc.	nucleus accumbens
n. bas. am.	nucleus basalis amygdalae
n. bas. am. p. lat.	nucleus basalis amygdalae, pars lateralis
n. bas. am. p. med.	nucleus basalis amygdalae, pars medialis
n. Br.	nucleus of the diagonal band of Broca
n. caud.	nucleus caudatus
n. centr. am.	nucleus centralis amygdalae
n. comm ant.	bed nucleus of the commissura anterior
n. cort. am.	nucleus corticalis amygdalae

n lat am	nucleus lateralis amygdalae
n lat am p ant	nucleus lateralis amygdalae, pars anterior
n lat am p post	nucleus lateralis amygdalae, pars posterior
n lat sept	nucleus lateralis septi
n med am	nucleus medialis amygdalae
n med sept	nucleus medialis septi
n str t	bed nucleus of the stria terminalis
n tr olf lat	nucleus of the tractus olfactorius lateralis
n tr olf lat p lat	nucleus of the tractus olfactorius lateralis, pars lateralis
n tr olf lat p med	nucleus of the tractus olfactorius lateralis, pars medialis
n triang sept	nucleus triangularis septi
parasub	parasubiculum
ped olf	pedunculus olfactorius
praesub	praesubiculum
put	putamen
r entorh	regio entorhinalis
r infr	regio infraradiata
r ins	regio insularis
r. occ	regio occipitalis
r par	regio parietalis
r perirh	regio perirhinalis
r postc	regio postcentralis
r praec agr	regio praecentralis agranularis
r praec gr	regio praecentralis granularis
r praep	regio praepiriformis
r retrosp	regio retrosplenialis
r temp	regio temporalis
str t	stria terminalis
str t p comm	stria terminalis, pars commissuralis
sub	subiculum
t olf	tuberculum olfactorium
thal	thalamus
tr olf lat	tractus olfactorius lateralis
tr op	tractus opticus
v III	ventriculus III
v lat	ventriculus lateralis
v olf	ventriculus olfactorius

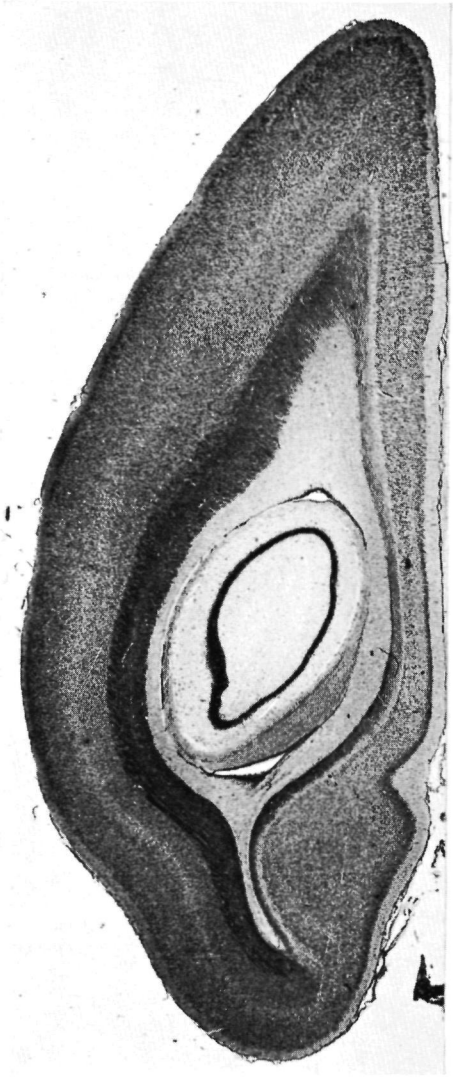


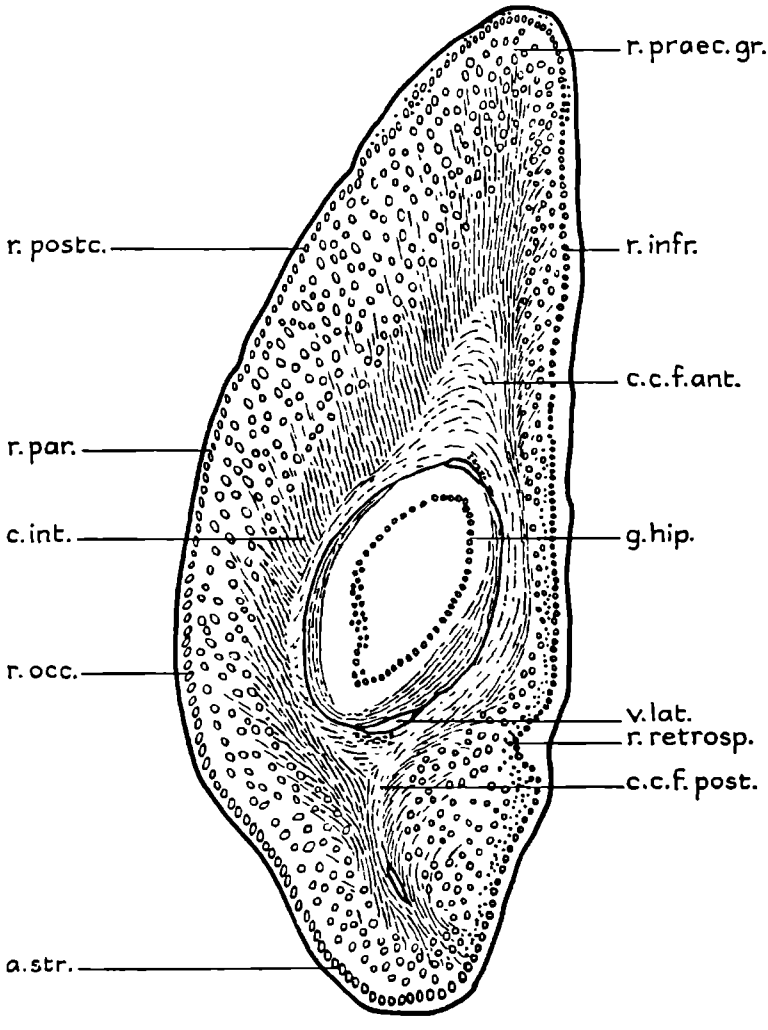
The brain of the adult rabbit. Lateral view (above), ventral view (middle), dorsal view (below).



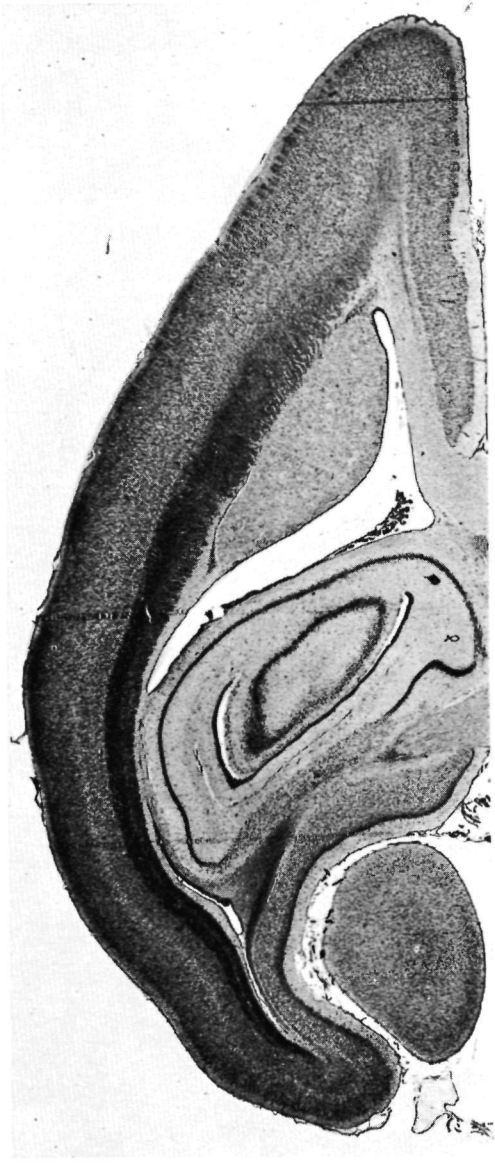


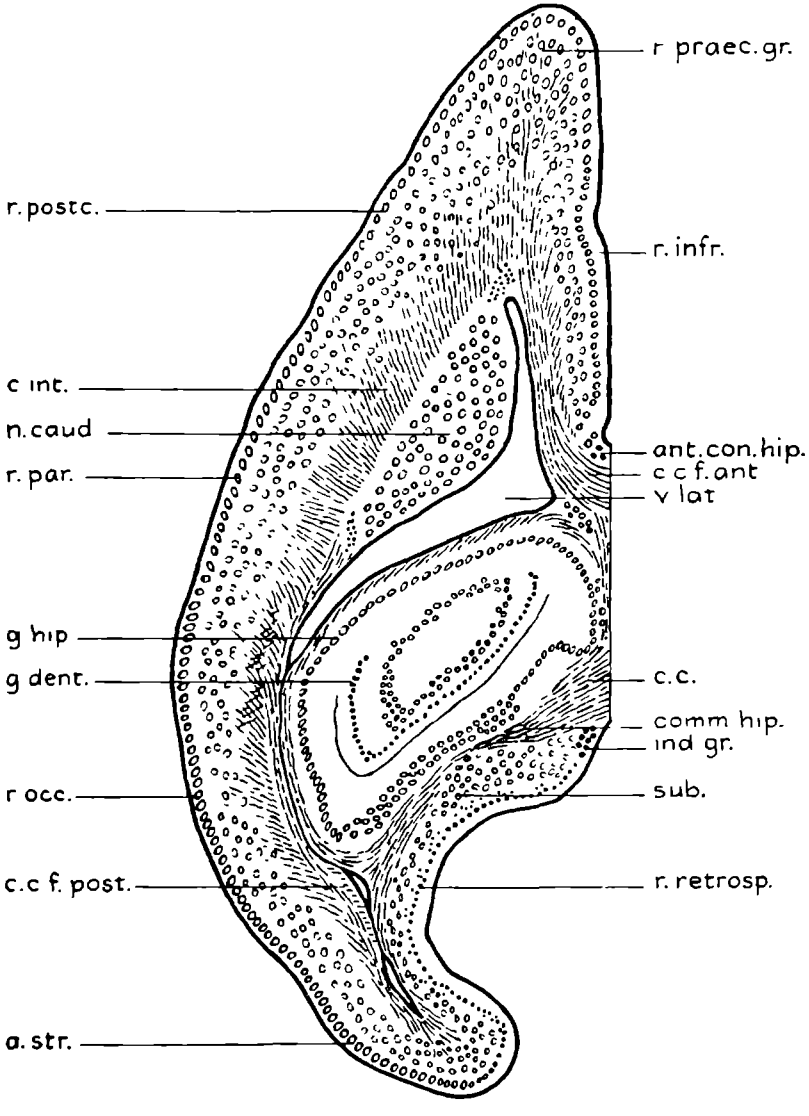
In the figures above, the levels of the horizontal and transverse sections in the atlas and in the figs. 1–18 are indicated. In the atlas the horizontal sections are reproduced on pages 32–63 from dorsal to ventral successively, the transverse sections on pages 64–67 from rostral to caudal successively. For technical comments see page 16.



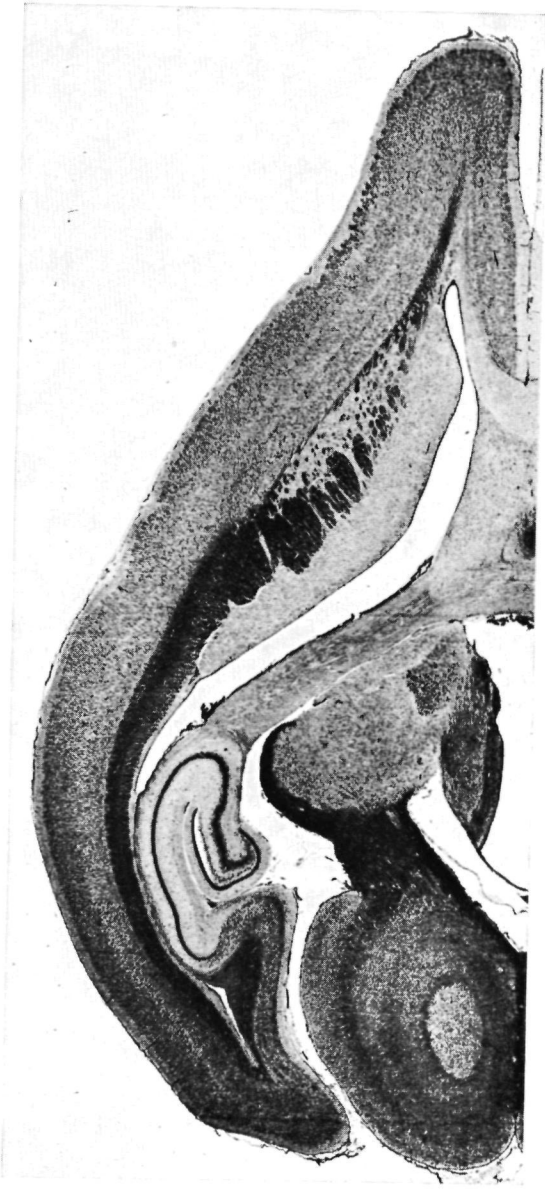

r. praec. gr.
r. postc.
r. infr.
c.c.f.ant.
r. par.
c. int.
g. hip.
r. occ.
v. lat.
r. retrosp.
c.c.f. post.
a. str.

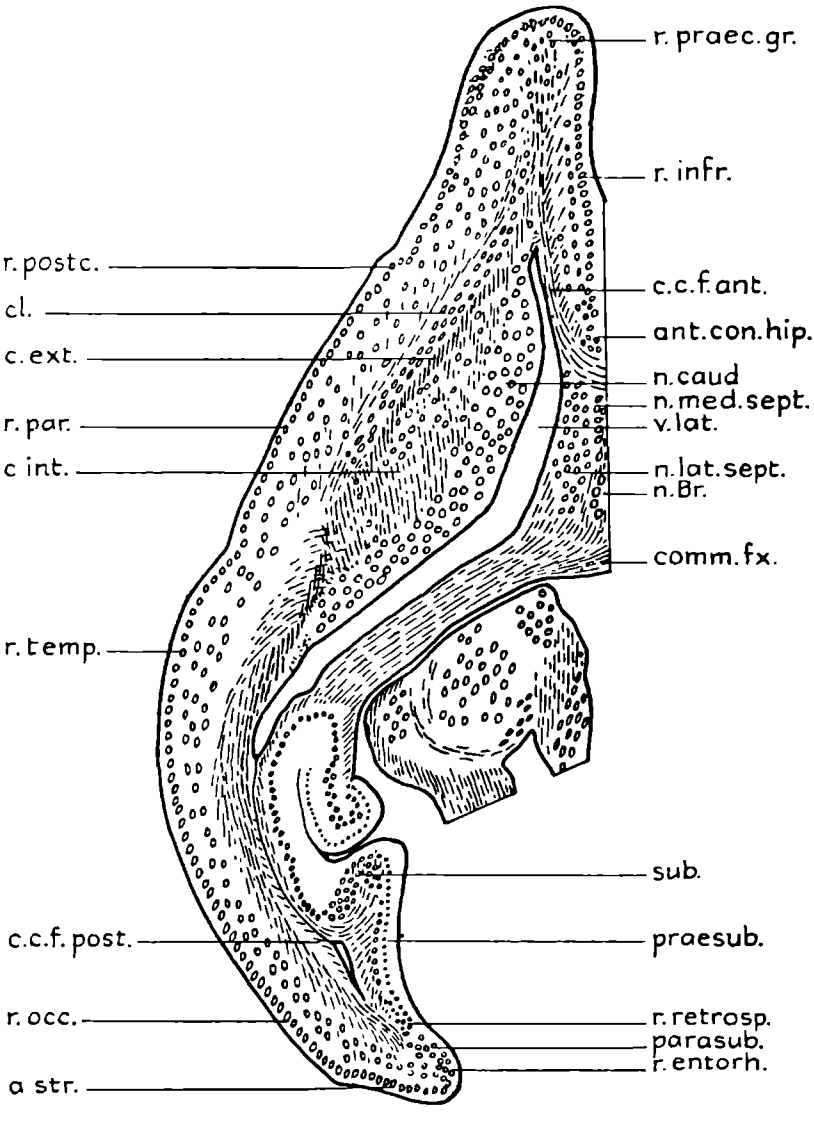
140



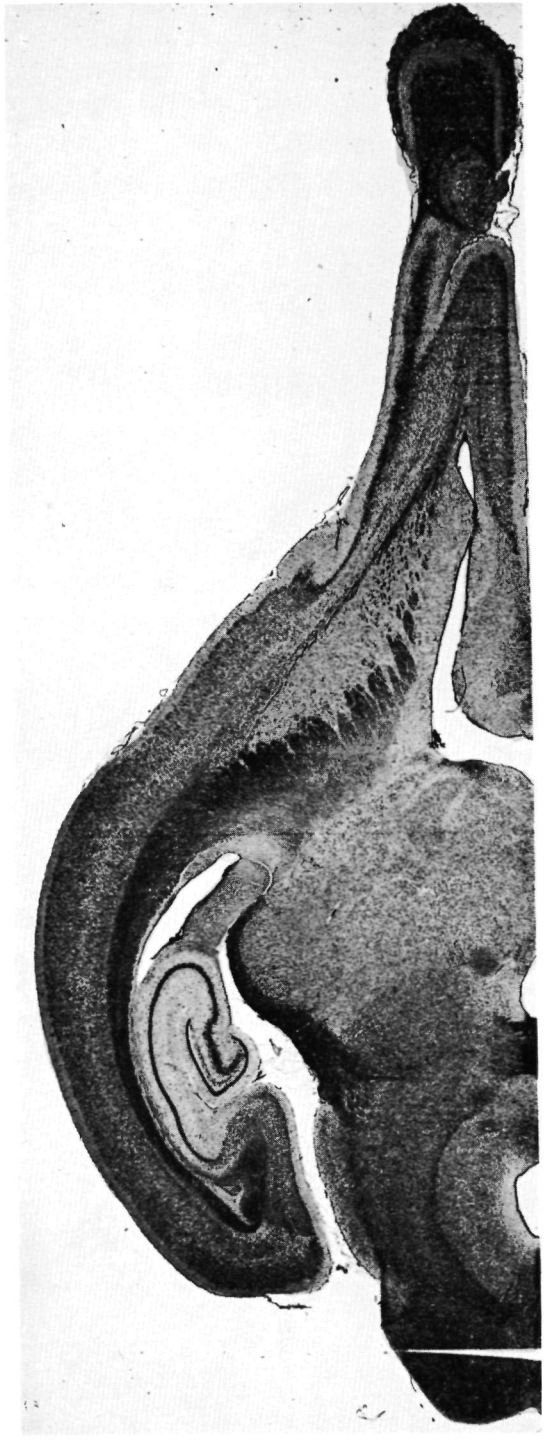

r praec. gr.
r. postc.
r. infr.
c int.
n. caud
r. par.
ant. con. hip.
c c f. ant
v lat
g hip
g dent.
c.c.
comm hip.
ind gr.
r occ.
sub.
c.c f. post.
r. retrosp.
a. str.

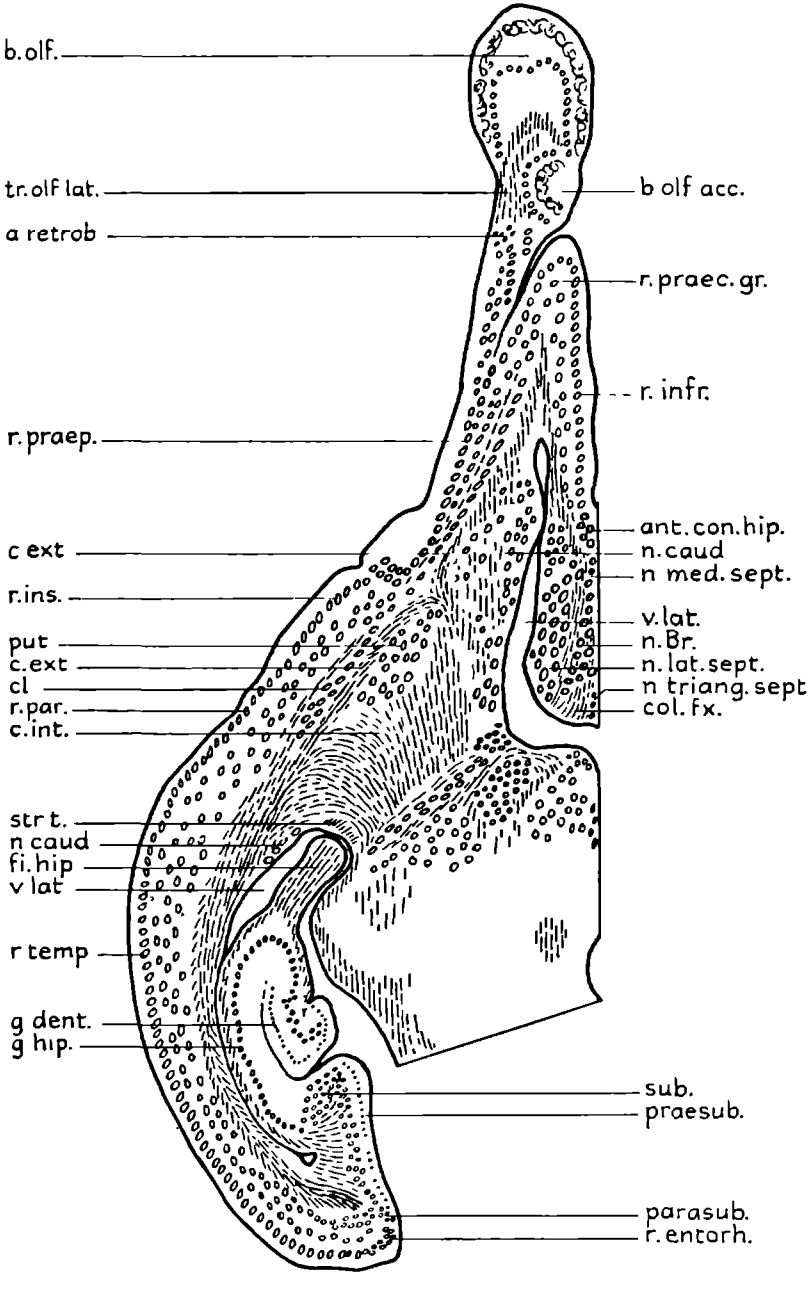
220



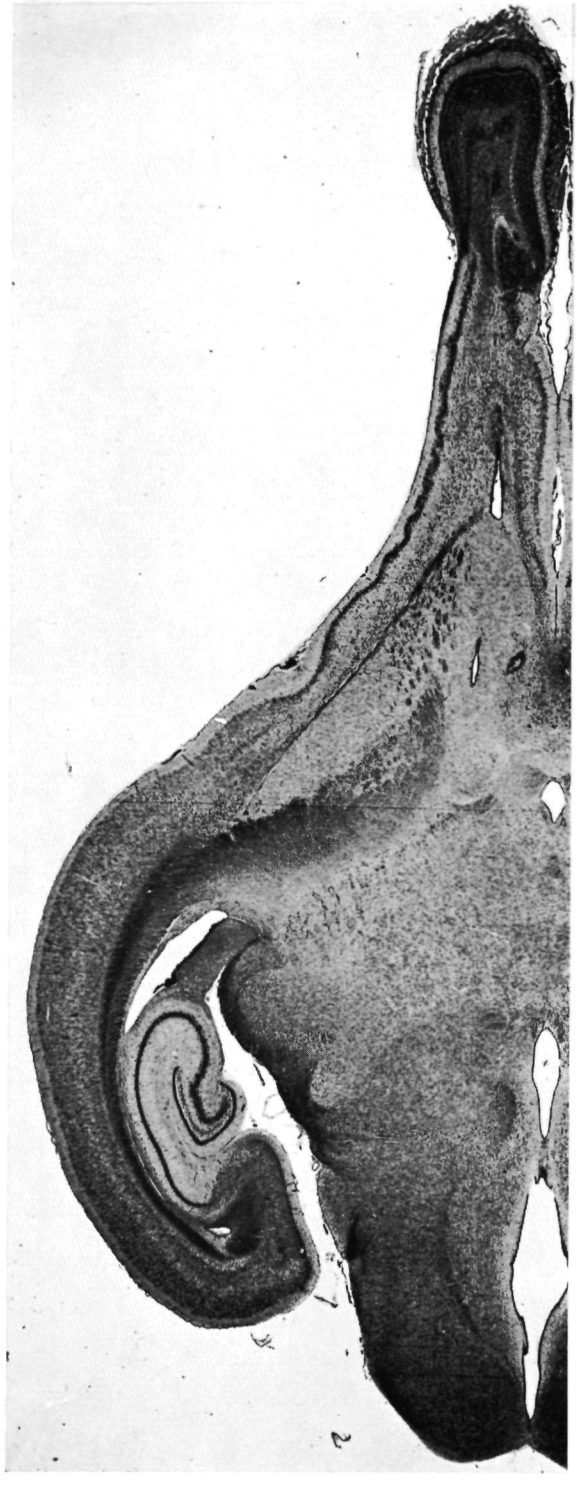

r. praec. gr.
r. infr.
r. postc.
cl.
c. ext.
r. par.
c int.
c.c.f. ant.
ant. con. hip.
n. caud
n. med. sept.
v. lat.
n. lat. sept.
n. Br.
comm. fx.
r. temp.
sub.
c.c.f. post.
praesub.
r. occ.
r. retrosp.
parasub.
r. entorh.
a str.

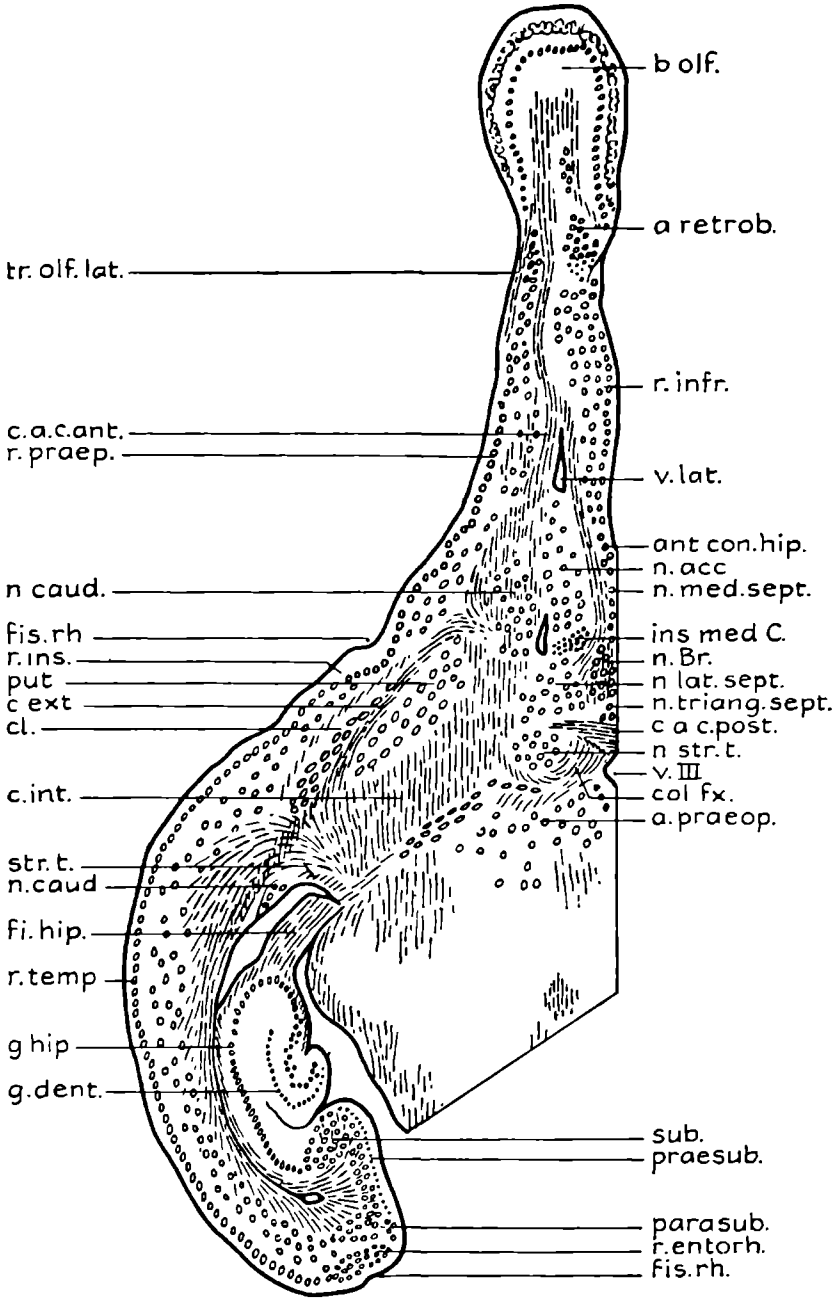
300



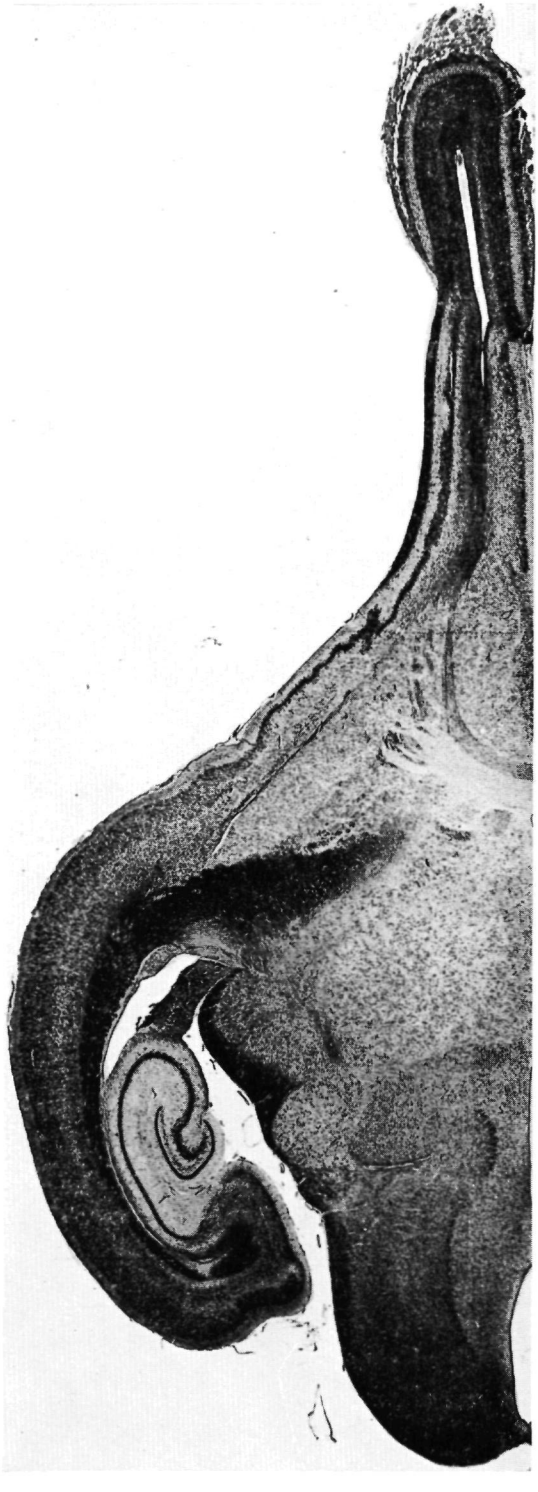

b. olf.
tr. olf lat.
a retrob
r. praep.
c ext
r. ins.
put
c. ext
cl
r. par.
c. int.
str t.
n caud
fi. hip
v lat
r temp
g dent.
g hip.
b olf acc.
r. praec. gr.
r. infr.
ant. con. hip.
n. caud
n med. sept.
v. lat.
n. Br.
n. lat. sept.
n triang. sept
col. fx.
sub.
praesub.
parasub.
r. entorh.

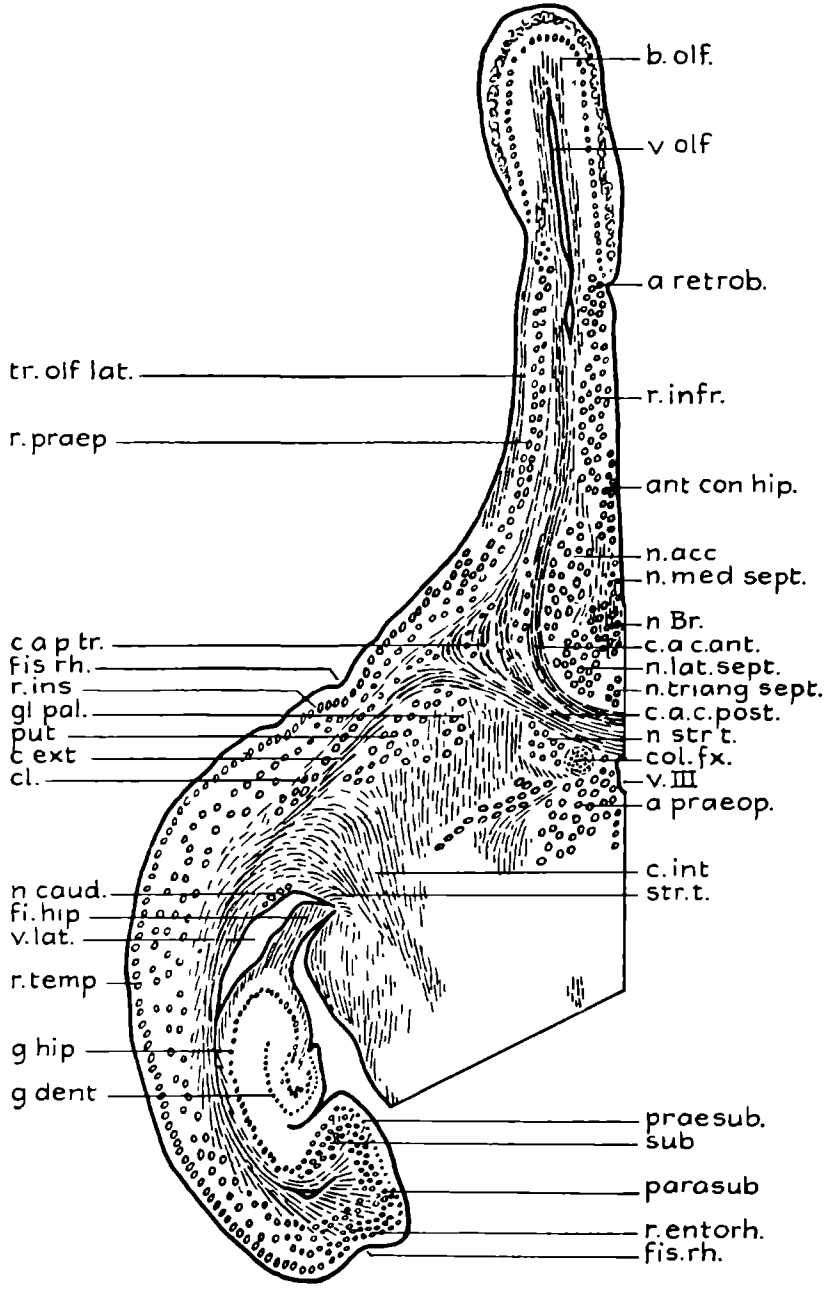
380



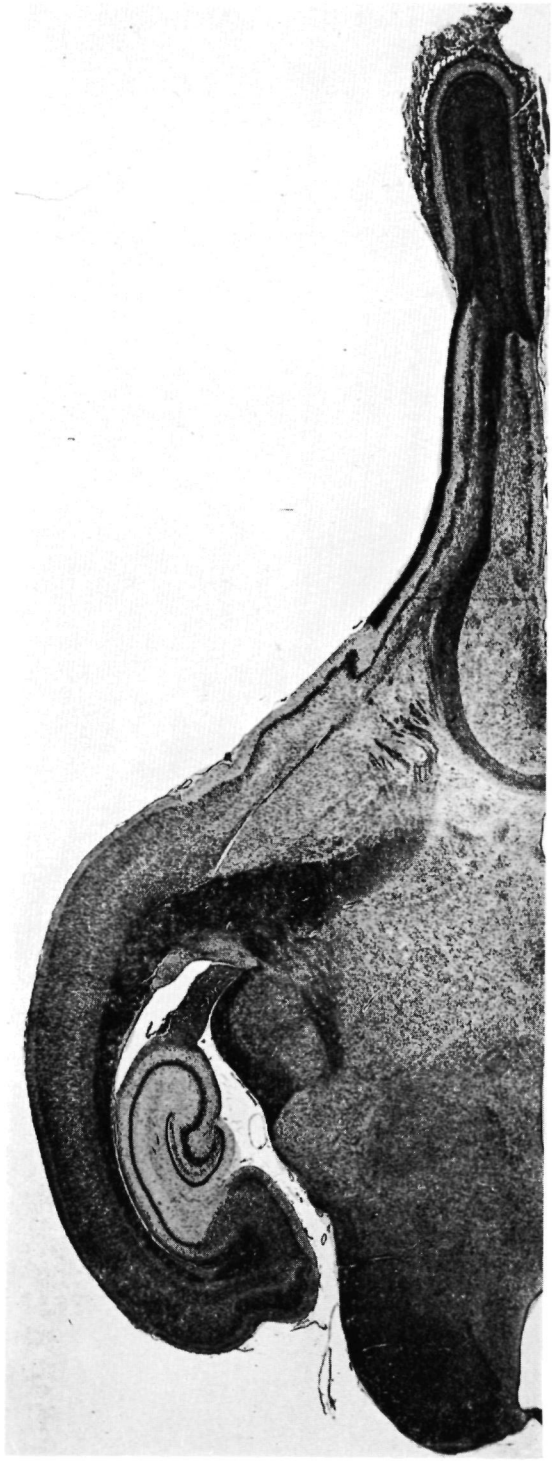

b olf.
a retrob.
tr. olf. lat.
r. infr.
c.a.c.ant.
r. praep.
v. lat.
ant con.hip.
n. acc
n caud.
n. med.sept.
fis.rh
ins med C.
r. ins.
n. Br.
put
n lat. sept.
c ext
n. triang. sept.
cl.
c a c.post.
n str. t.
v. III
c.int.
col fx.
a. praeop.
str. t.
n.caud
fi. hip.
r. temp
g hip
g.dent.
sub.
praesub.
parasub.
r. entorh.
fis. rh.

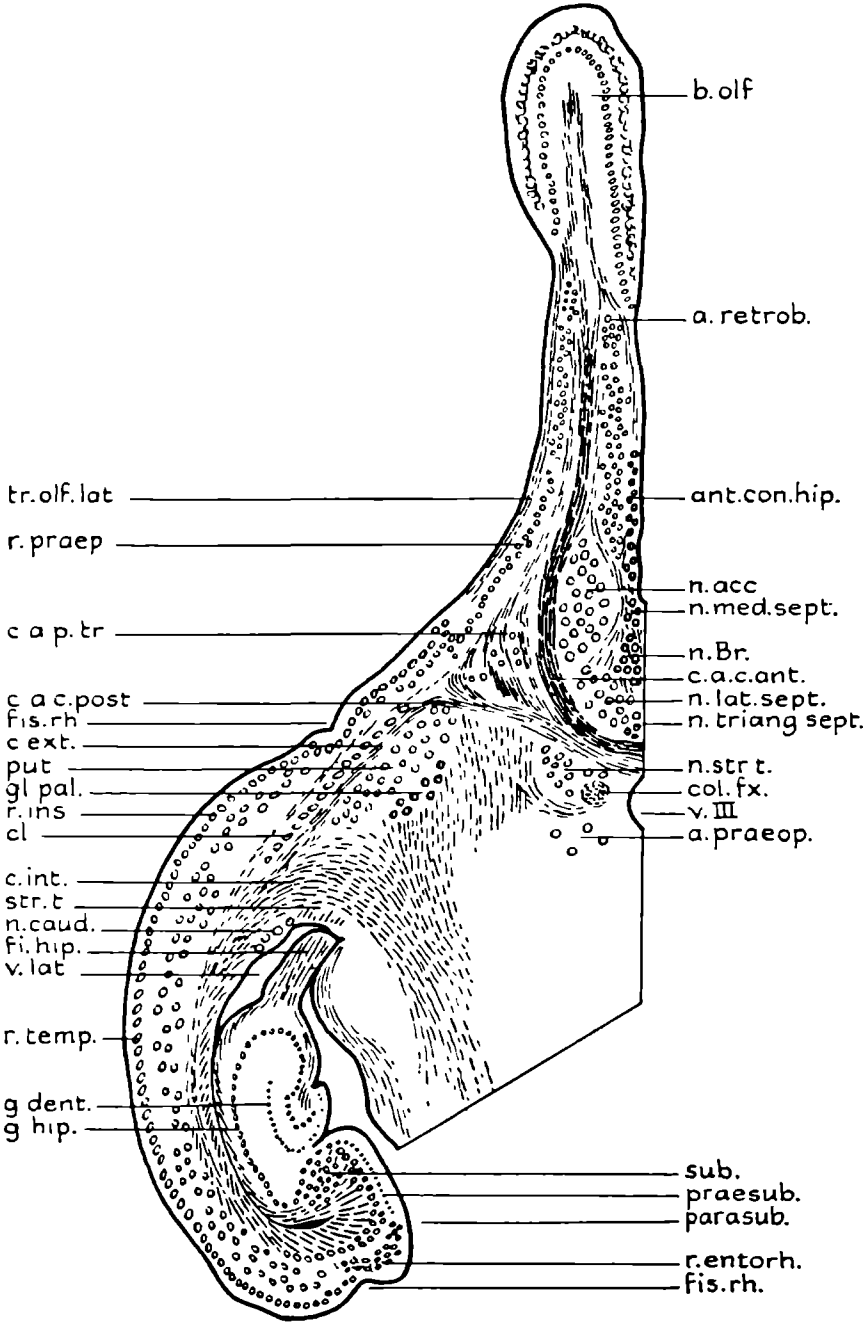
420



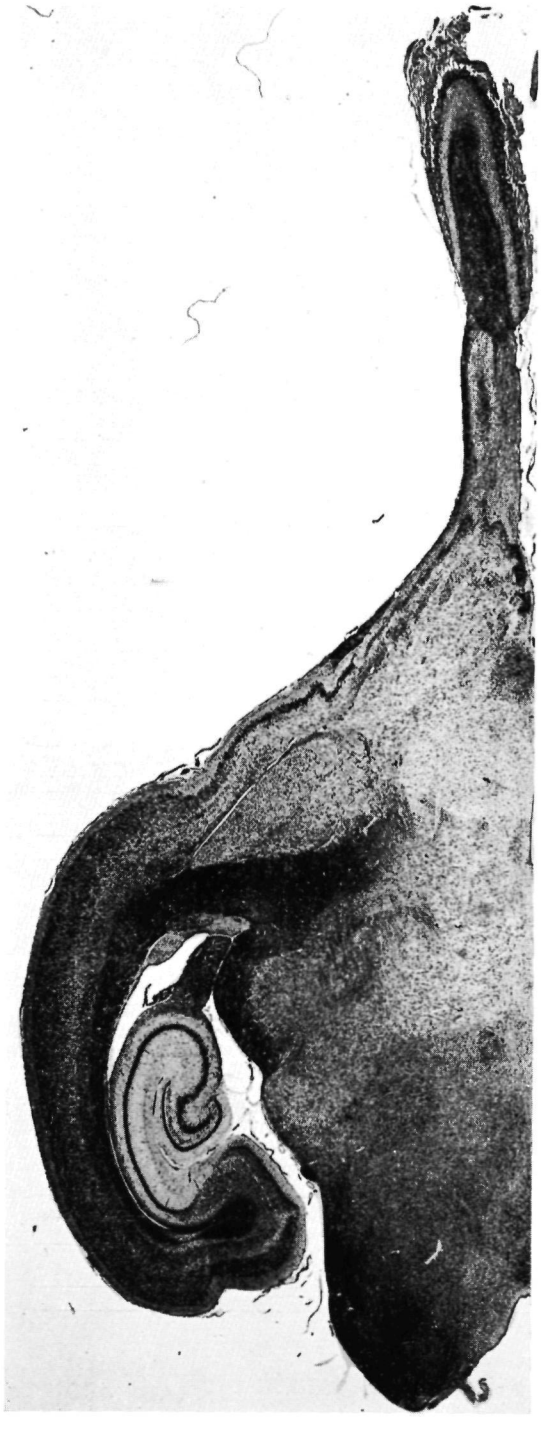

b. olf.
v olf
a retrob.
tr. olf lat.
r. infr.
r. praep
ant con hip.
n. acc
n. med sept.
n Br.
c a p tr.
c. a c. ant.
fis rh.
n. lat. sept.
r. ins
n. triang sept.
gl pal.
c. a. c. post.
put
n str t.
t ext
col. fx.
cl.
v. III
a praeop.
c. int
n caud.
str. t.
fi. hip
v. lat.
r. temp
g hip
g dent
praesub.
sub
parasub
r. entorh.
fis. rh.

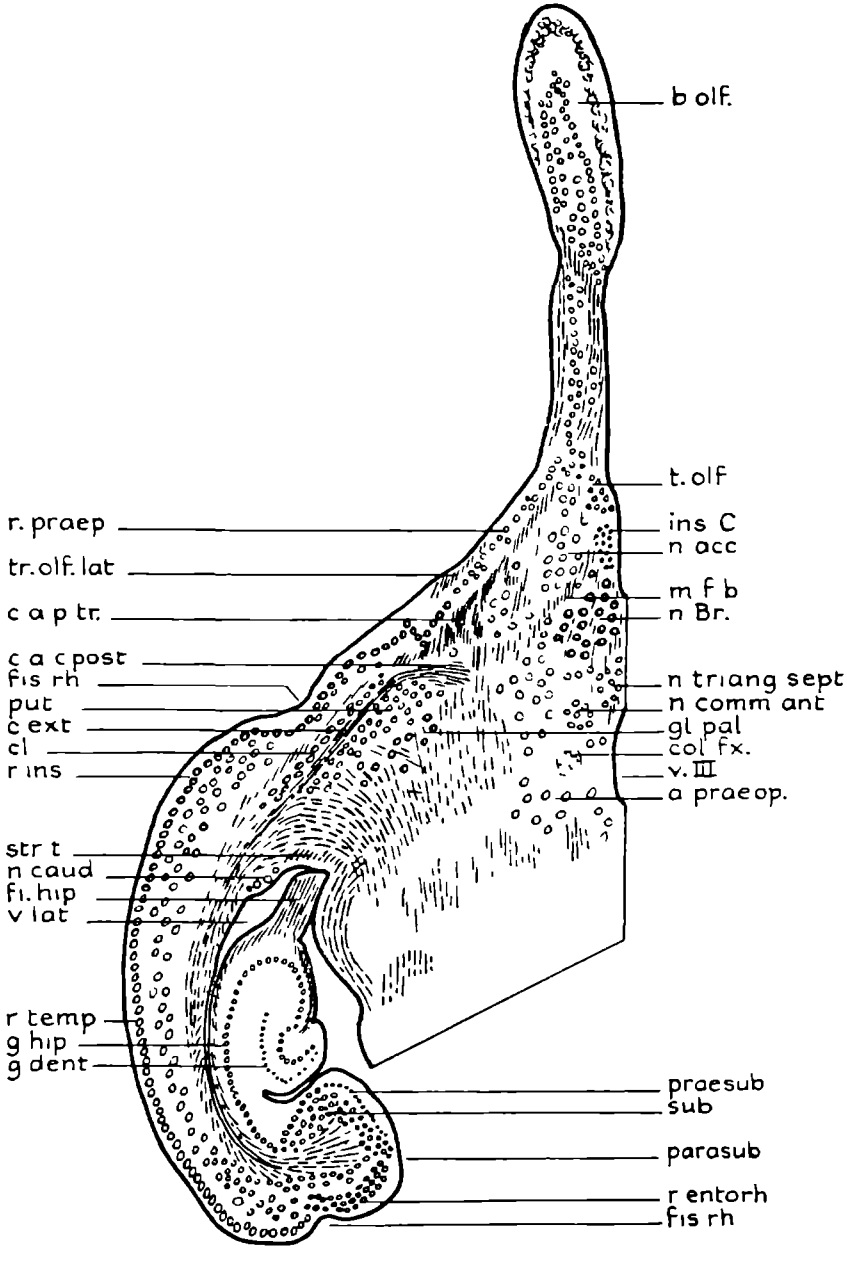
460



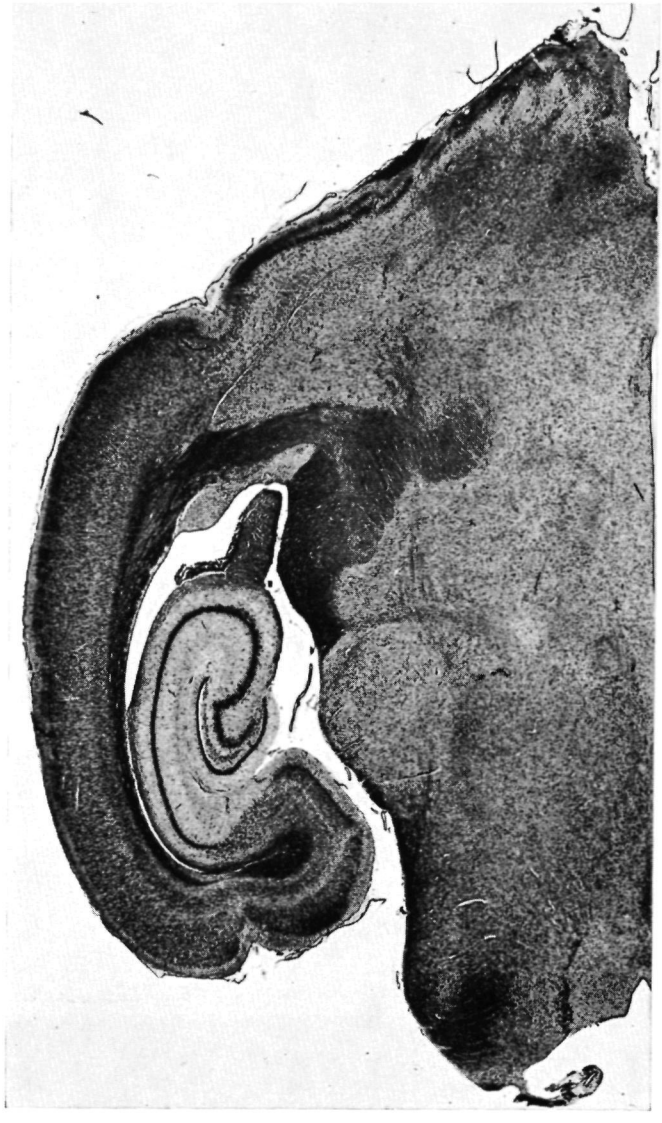

b. olf
a. retrob.
tr. olf. lat
r. praep
c a p. tr
c a c. post
fis. rh
c ext.
put
gl pal.
r. ins
cl
c. int.
str. t
n. caud.
fi. hip.
v. lat
r. temp.
g dent.
g hip.
ant. con. hip.
n. acc
n. med. sept.
n. Br.
c. a. c. ant.
n. lat. sept.
n. triang sept.
n. str t.
col. fx.
v. III
a. praeop.
sub.
praesub.
parasub.
r. entorh.
fis. rh.

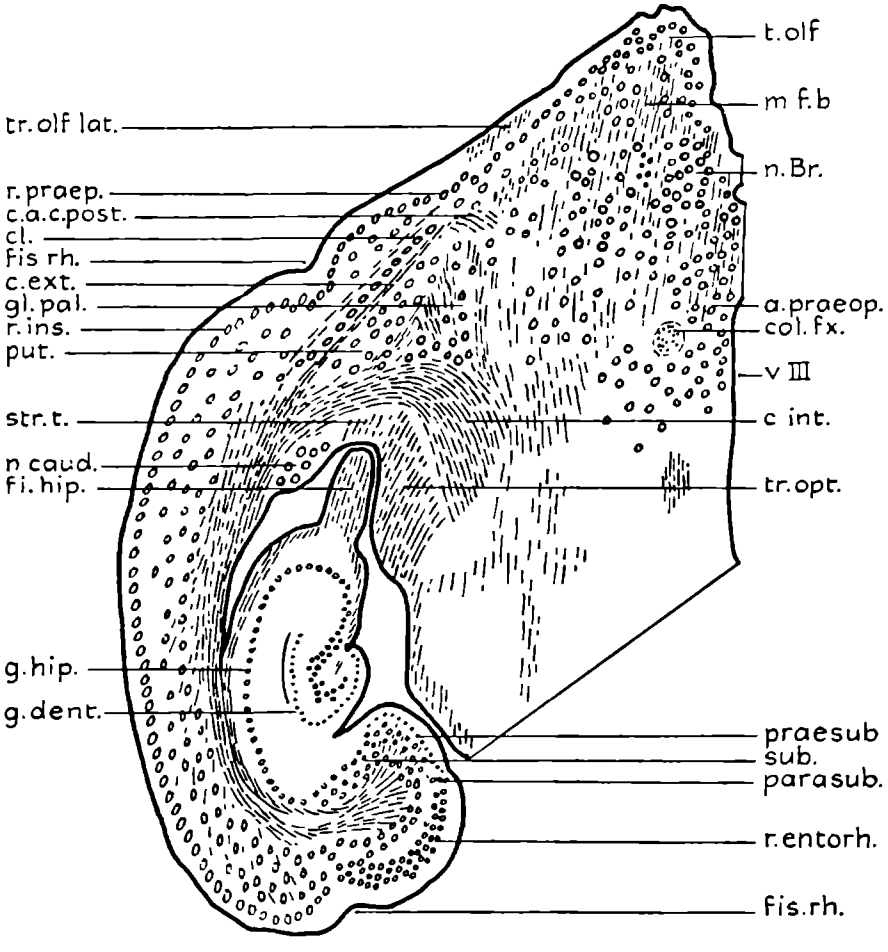
480



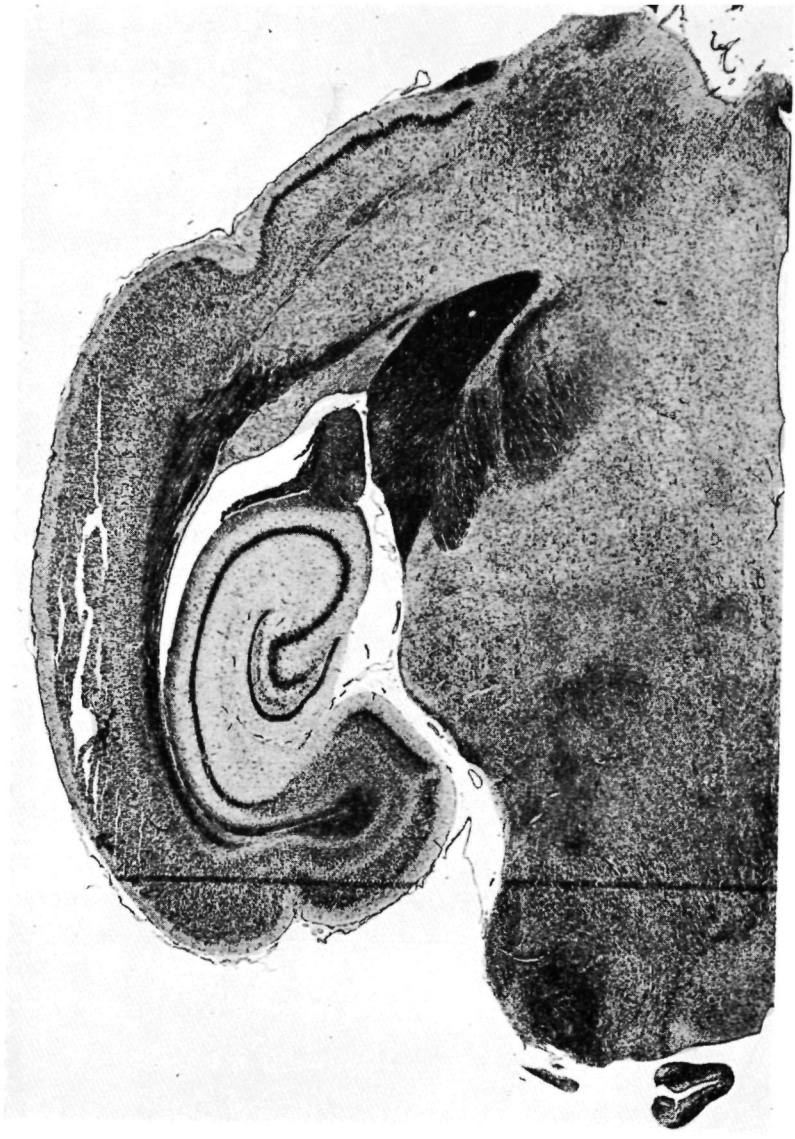

b olf.
t. olf
r. praep
ins C
n acc
tr. olf. lat
m f b
c a p tr.
n Br.
c a c post
fis rh
n triang sept
put
n comm ant
c ext
gl pal
cl
col fx.
r ins
v. III
a praeop.
str t
n caud
fi. hip
v lat
r temp
g hip
g dent
praesub
sub
parasub
r entorh
fis rh

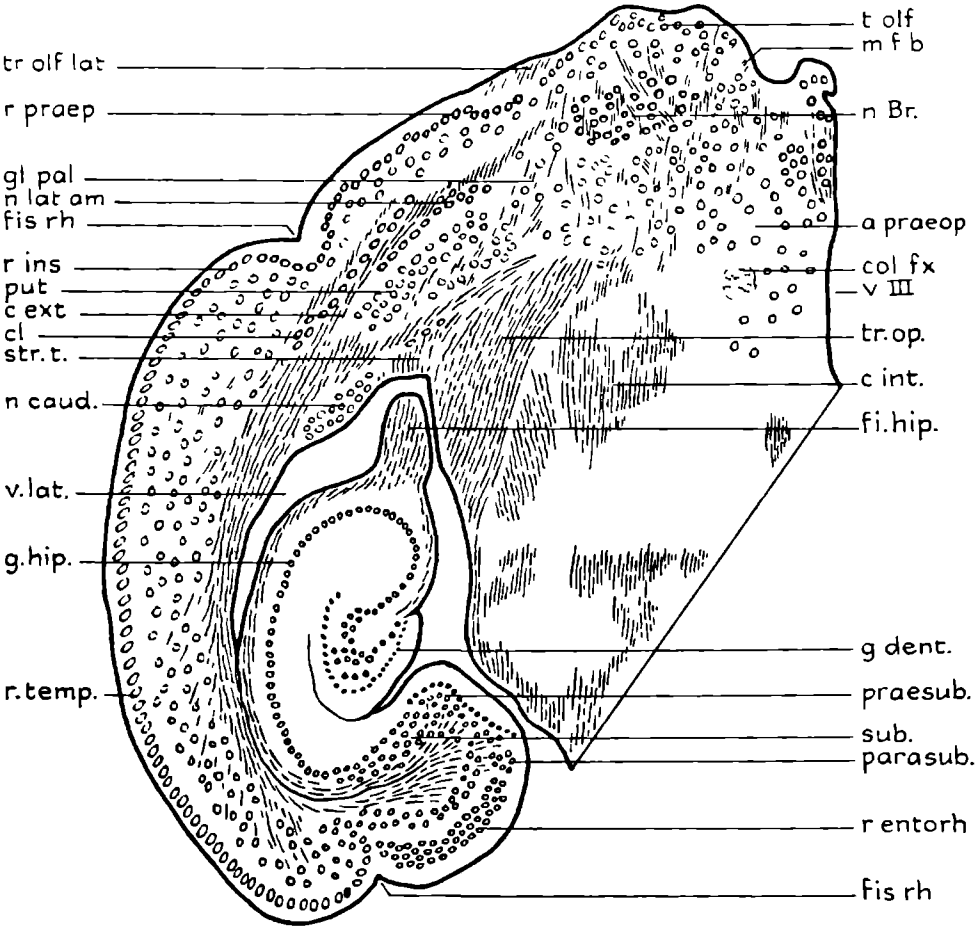
520



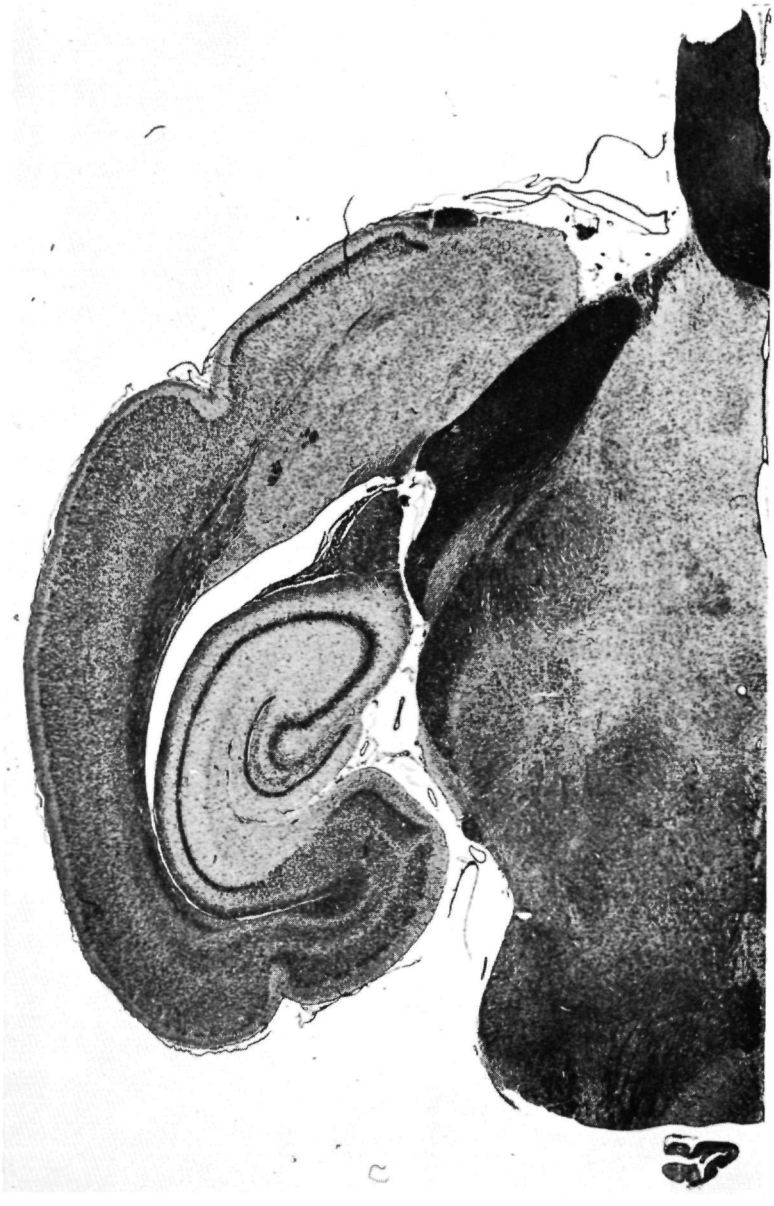

t.olf
m f.b
n.Br.
a.praeop.
col.fx.
v III
c int.
tr.opt.
praesub
sub.
parasub.
r.entorh.
fis.rh.
tr.olf lat.
r.praep.
c.a.c.post.
cl.
fis rh.
c.ext.
gl.pal.
r.ins.
put.
str.t.
n caud.
fi.hip.
g.hip.
g.dent.

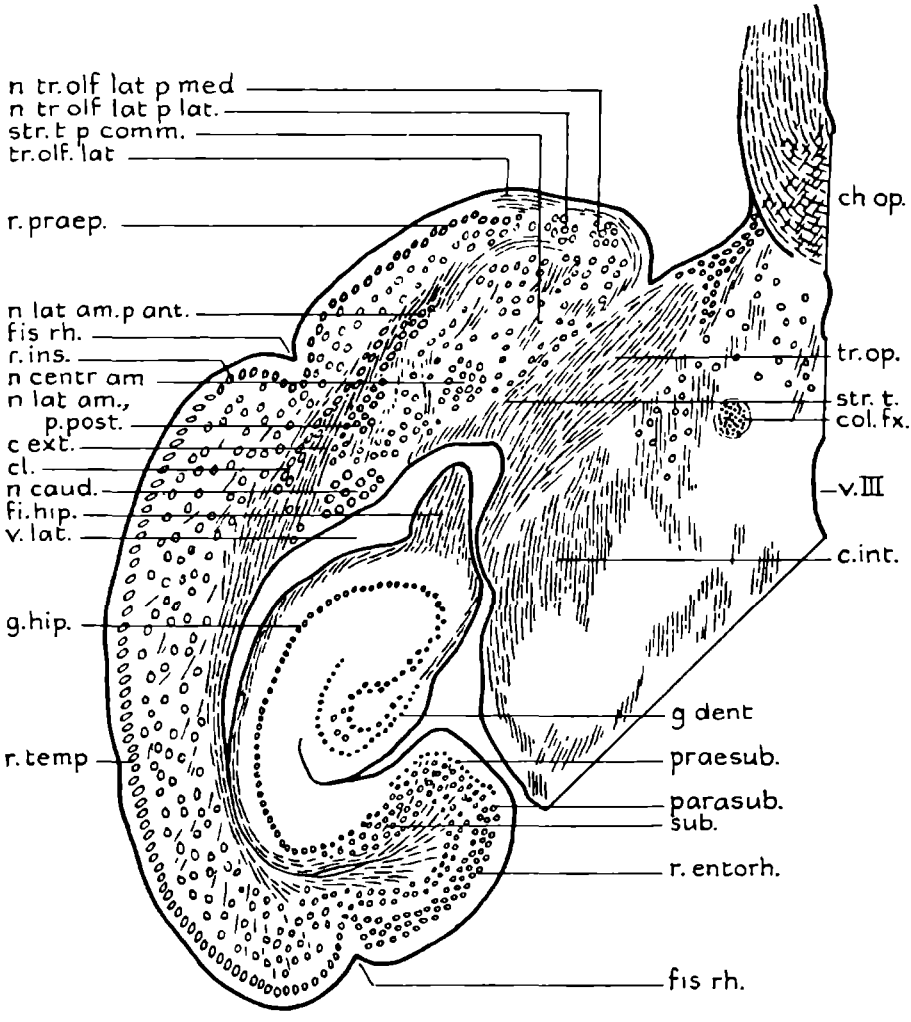
560



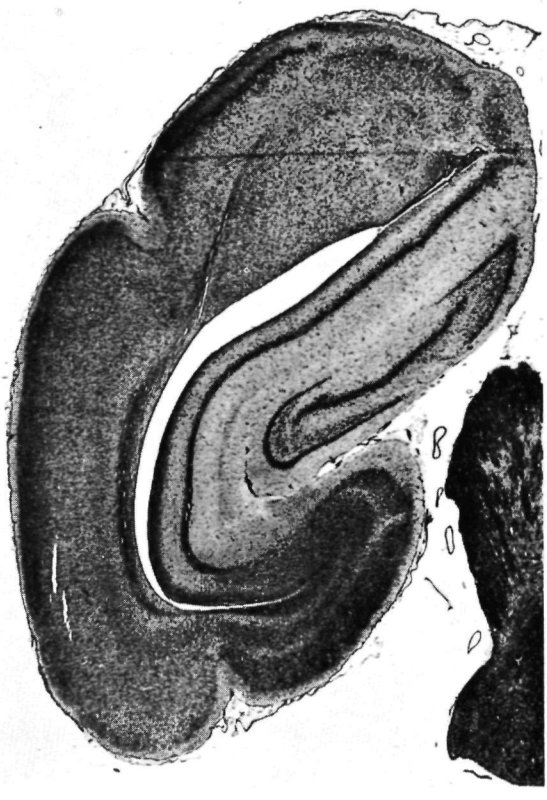

t olf
m f b
tr olf lat
r praep
n Br.
gl pal
n lat am
fis rh
a praeop
r ins
col fx
put
v III
c ext
cl
tr. op.
str. t.
c int.
n caud.
fi. hip.
v. lat.
g. hip.
g dent.
r. temp.
praesub.
sub.
parasub.
r entorh
fis rh

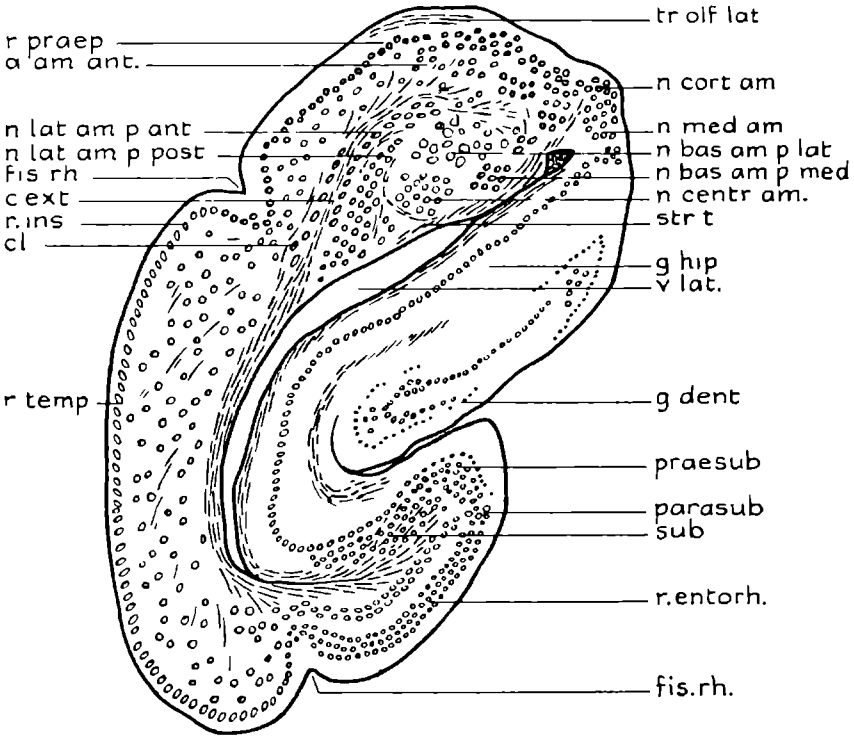
600



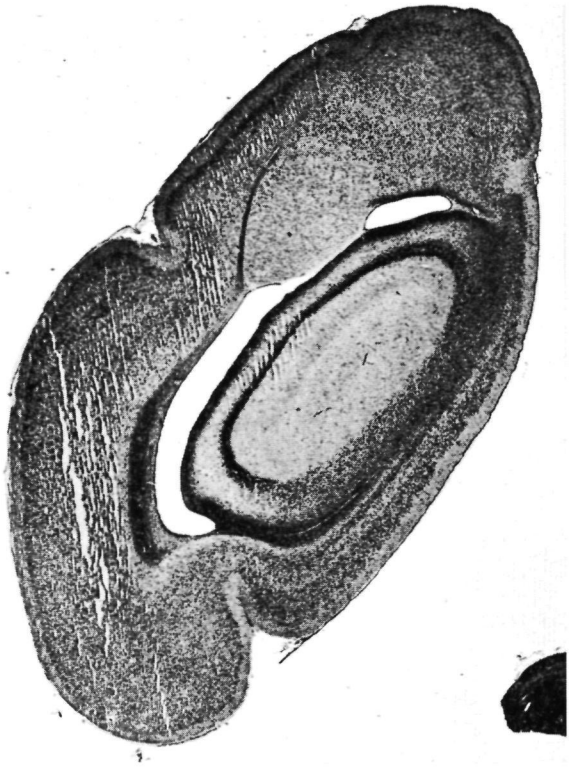

n tr.olf lat p med
n tr olf lat p lat.
str. t p comm.
tr.olf. lat
r. praep.
n lat am.p ant.
fis rh.
r. ins.
n centr am
n lat am.,
p.post.
c ext.
cl.
n caud.
fi. hip.
v. lat.
g.hip.
r. temp
ch op.
tr.op.
str. t.
col. fx.
v. III
c.int.
g dent
praesub.
parasub.
sub.
r. entorh.
fis rh.

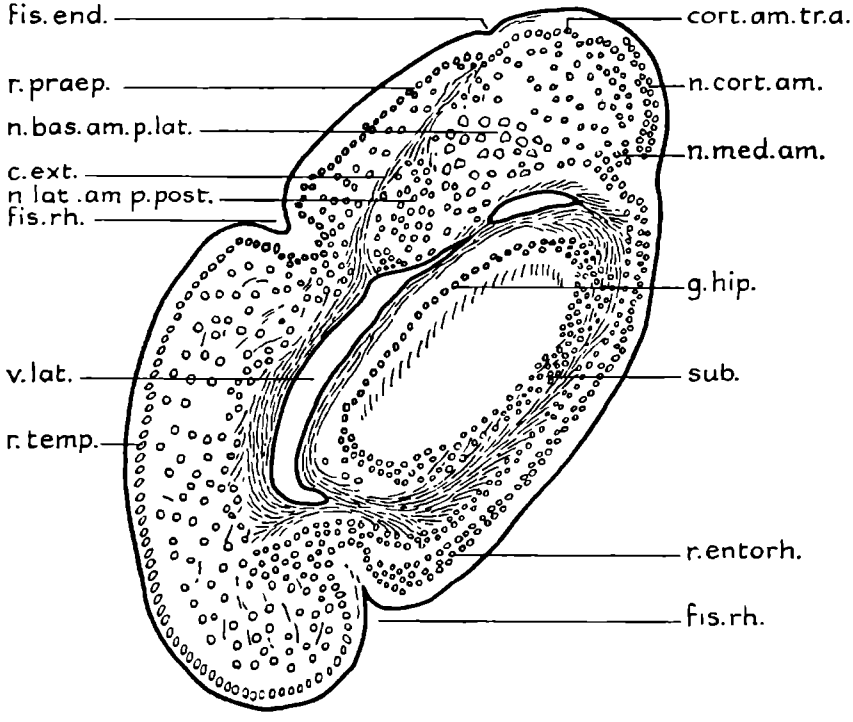
640



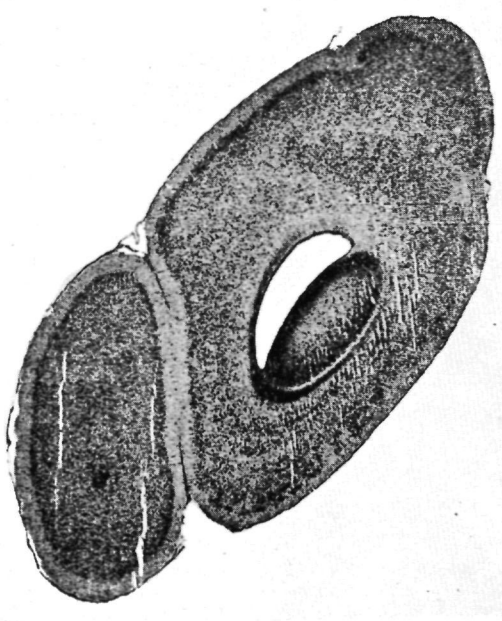

r praep
a am ant.
n lat am p ant
n lat am p post
fis rh
c ext
r.ins
cl
r temp
tr olf lat
n cort am
n med am
n bas am p lat
n bas am p med
n centr am.
str t
g hip
v lat.
g dent
praesub
parasub
sub
r.entorh.
fis.rh.

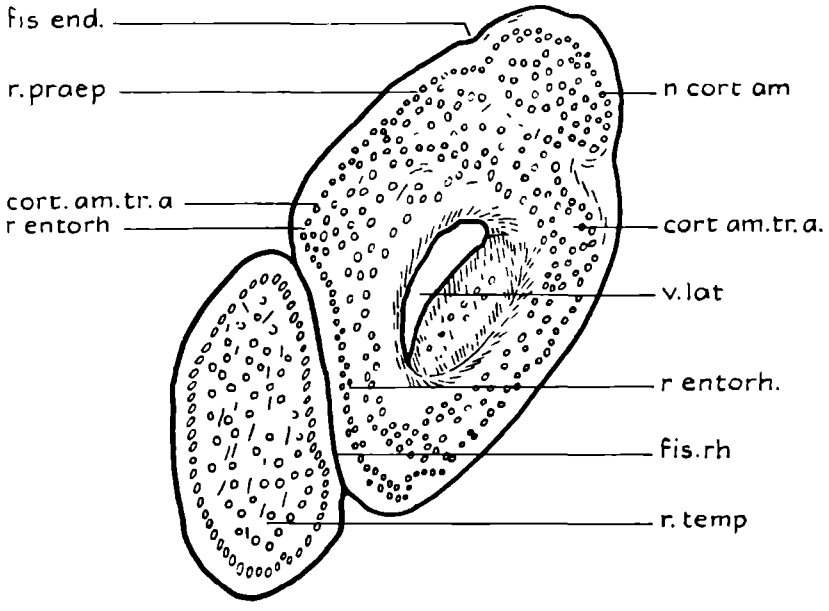
720



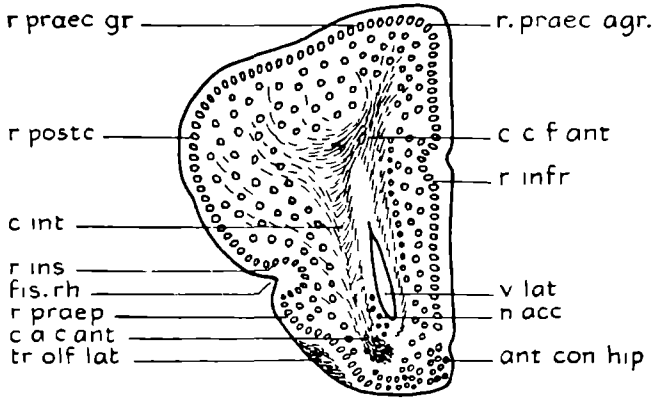

fis. end.
r. praep.
n. bas. am. p. lat.
c. ext.
n lat. am p. post.
fis. rh.
v. lat.
r. temp.
cort. am. tr. a.
n. cort. am.
n. med. am.
g. hip.
sub.
r. entorh.
fis. rh.

790

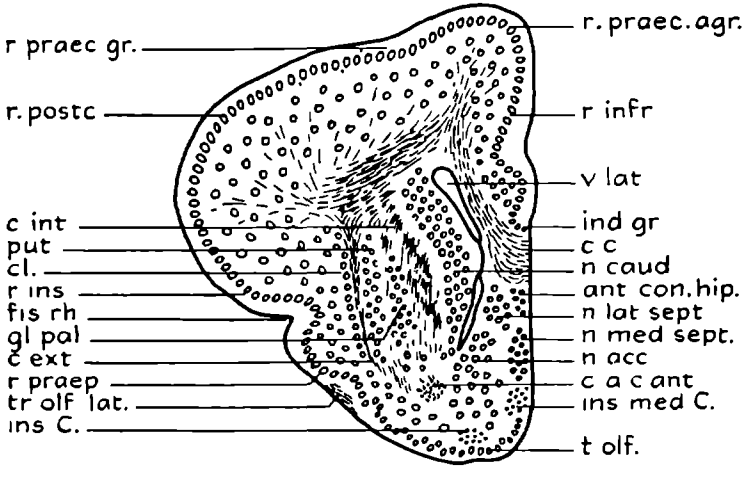



fis end.
r. praep
cort. am. tr. a
r entorh
n cort am
cort am. tr. a.
v. lat
r entorh.
fis. rh
r. temp

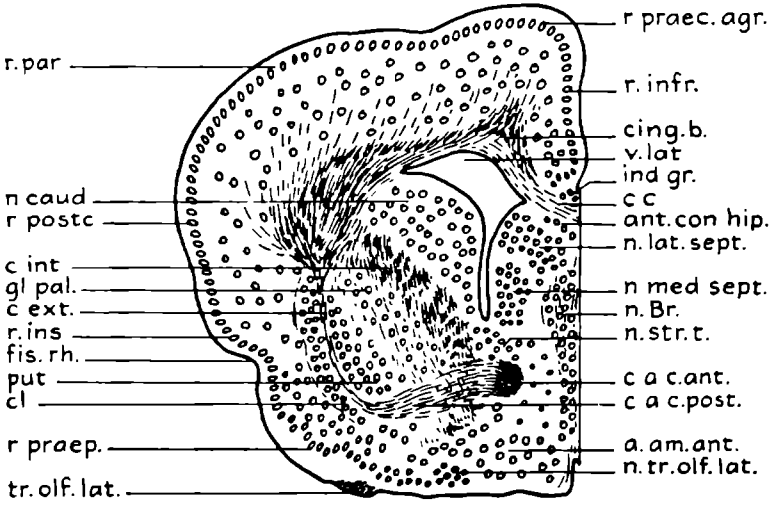
830


r praec gr
r. praec agr.
r postc
c c f ant
r infr
c int
r ins
fis. rh
v lat
r praep
n acc
c a c ant
tr olf lat
ant con hip

250


r praec gr.
r. praec. agr.
r. postc
r infr
v lat
c int
ind gr
put
c c
cl.
n caud
r ins
ant con. hip.
fis rh
n lat sept
gl pal
n med sept.
c ext
n acc
r praep
c a c ant
tr olf lat.
ins med C.
ins C.
t olf.

350


r praec. agr.
r. par
r. infr.
cing. b.
v. lat
ind gr.
n caud
c c
r postc
ant. con hip.
n. lat. sept.
c int
gl pal.
n med sept.
c ext.
n. Br.
r. ins
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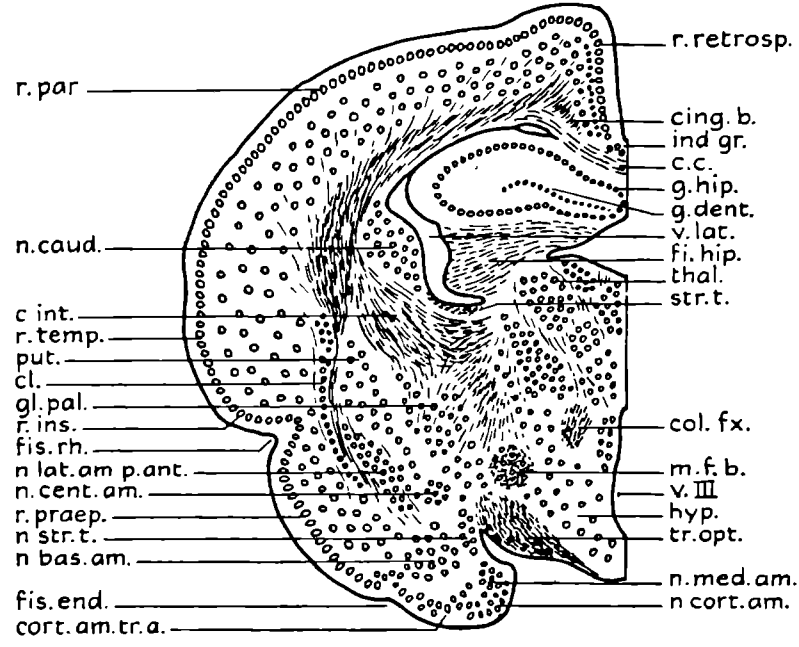
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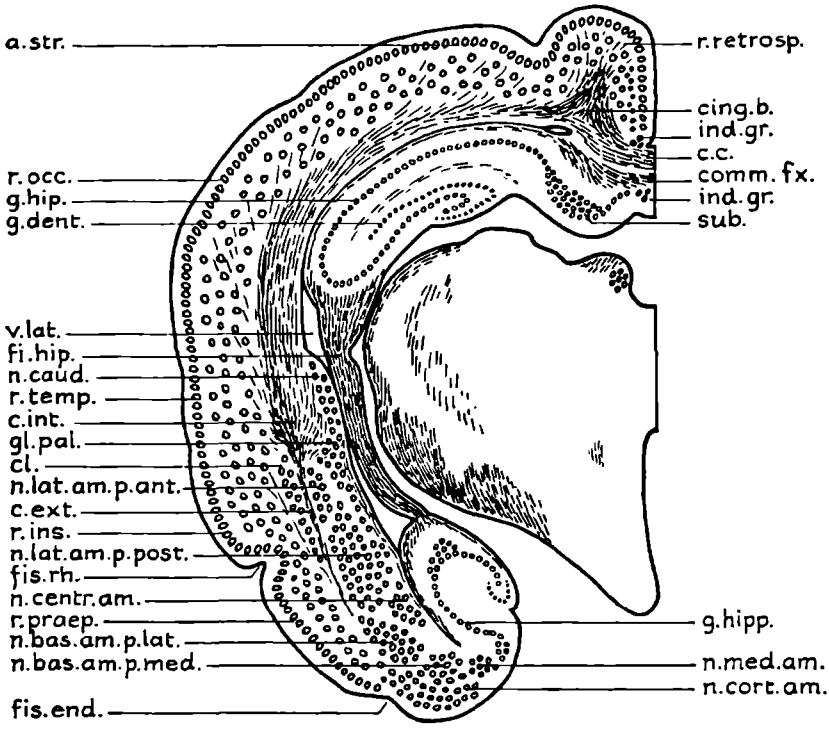
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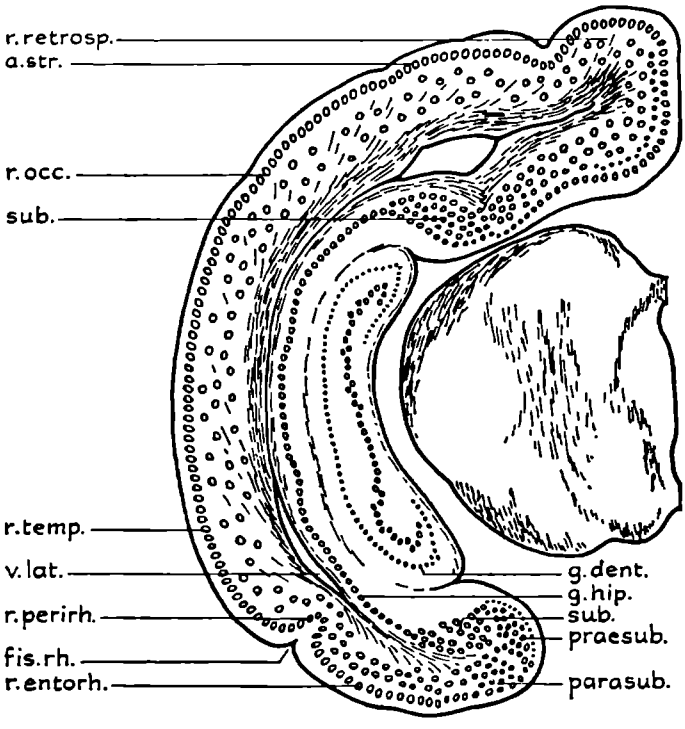
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Part II

EXPERIMENTAL ANATOMICAL STUDY OF THE POSTERIOR LIMB AND THE STRIA TERMINALIS COMPONENT OF THE ANTERIOR COMMISSURE

SURVEY OF THE LITERATURE

As described in the preceding section, three components can be distinguished in the anterior commissure: the anterior limb, the posterior limb and the pars ad striam terminalem. Meynert (1870, 1872) had already noted in lower animals that the anterior limb is much more developed than the posterior limb, whereas the inverse is the case in monkey and man. Meynert compared this with the development of the olfactory bulb and believed that 'nothwendigerweise auch wirkliche Commissurenbündel derselben sowohl beide Riechlappen, als beide Hemisphären miteinander verbinden.' The same investigator posed the question which he answered in the affirmative 'ob zwischen den aus dem Riechlappen hervorgehenden und den zur Grosshirnrinde gelangenden Bündeln eine Continuität bestehe, sodass Theile des Riechlappenmarkes durch die vordere Commissur zum entgegengesetzten Schläfen- und Hinterhauptlappen gelangen?' On the analogy of the optic chiasma Meynert coined the term 'Riechchiasma.'

At the same time, Gudden (1870) and Ganser (1879), using the atrophy method in experimental studies in rabbits, were unable to demonstrate the decussation of the two components of the anterior commissure as suggested by Meynert. Subsequently, other workers also convincingly showed that crossing-over does not occur. The anterior and posterior limbs must be regarded as two distinct fibre pathways (Edinger, 1893; Kolliker, 1896; Loewenthal, 1897; Probst, 1901; Kreiner, 1936).

These findings do not, however, justify the conclusion drawn by the last-mentioned authors, namely that the two components consist of true commissural fibres which connect homologous areas on both sides of the midline. Doubts about the true commissural nature of the anterior limb had already been expressed by Loewenthal (1897). Van Gehuchten (1904) was able to

demonstrate by Marchi studies that 'la partie olfactive de la commissure blanche antérieure ne peut pas être considérée comme une véritable commissure reliant l'une à l'autre des parties homologues des deux hémisphères, mais plutôt comme un entrecroisement des fibres d'association reliant les cellules du lobe olfactif d'un côté aux cellules du bulbe olfactif du côté opposé.' More detailed data about the origin and termination of the anterior limb were obtained after introduction of Nauta's silver impregnation method (Lammers, 1959; Lohman and Lammers, 1961, 1963, 1967; Lohman, 1963; Powell, Cowan and Raisman, 1965; Scalia, 1966; Lohman and Mentink, 1966, 1969; Heimer, 1968a).

The posterior limb of the anterior commissure

The posterior limb of the anterior commissure owes its name, pars interhemispherica, to the hypothesis that this component might constitute a commissural connection between certain areas of the cerebral hemispheres. Observations regarding this problem on normal brains by early investigators were very accurate despite the limited technical means available. Burdach (1822) described the commissure as 'eine Verknüpfung von Hinter-, Unter- und Stammlappen beyder Hemisphären.' According to Gratiolet (1839–1857), the anterior commissure in man constitutes a connection between the complete cortex of one hemisphere and that of the other, whereas in the monkey only the two occipital poles are connected. Arnold (1851) and Luys (1865) only observed a distribution of the commissural fibres in the temporal poles. Foville (1844), however, considered that the anterior commissure was a crossed connection between the lentiform nucleus, the optic thalamus and the olfactory bulb on one side, and the cerebral cortex on the other. He believed that the fibres fanned out widely in the cortex. Cajal (1904) mentioned the caudal portion of the piriform cortex as a possible origin and termination of the fibres of the anterior commissure in the rat. Gurdjian (1925) demonstrated that 'the anterior commissure consists not only of the classical interbulbar and the intertemporal components, but of practically an unbroken extent of fibres, interrelating the bulbar and lateral secondary and tertiary olfactory areas (largely pyriform lobe) from the region of the olfactory bulb to practically the caudal end of the hemisphere'. However, Kreiner (1936), also in the rat, could only follow the fibres of the posterior limb into the piriform cortex, and, to a lesser extent into the claustrum. On the basis of a comparative anatomical study, Ariëns Kappers, Huber and Crosby (1936) distinguished in the intertemporal component of the anterior commissure, 1) an interpiriform part, 2) an interamygdaloid part which connect, respectively, the cortex of the piriform lobe

and the basal and lateral amygdaloid nuclei of one hemisphere with the corresponding areas on the heterolateral side, and 3) a neocortical component. The last component appeared best developed in those animals which lacked a corpus callosum, such as some monotremes and marsupials, and seemed to decrease in size in higher animals as the corpus callosum became better developed. However, even in the highest mammals there was still supposed to be a neocortical component in the anterior commissure. Similar observations were made by Johnston (1923) and Loo (1931) in the opossum, by Young (1936) in the rabbit, by Humphrey (1936) in the bat, and by Jeserich (1945) in the mink.

Experimental research on the anterior commissure started with the use of the atrophy method by Gudden (1870), Ganser (1879), and Winkler (1917). According to Gudden there is a genuine 'Hemisphärencommissur' which connects the two piriform lobes with one another. Ganser was of the opinion that the posterior limb contains a few fibres 'welche noch nicht näher begrenzte Rindengebiete der Schläfenlappen verknüpfen,' while Winkler also observed fibres terminating in the claustrum, the corpus striatum, the amygdaloid nucleus and the distal portions of Ammon's horn.

Experimental studies with the Marchi technique were made by Probst (1901) in the dog and the cat, by Poljak (1927), Fox (1943) and Fox and Schmitz (1943) in the cat, by Sunderland (1940) and Fox, Fisher and Desalva (1948) in the monkey, and by Ban and Omukai (1959) in the rabbit. Probst, after severing the posterior limb of the anterior commissure in the midline, was able to follow degenerated fibres in a lateral direction to the ventral projection of the external capsule where they spread out. Similarly to Ganser, Probst speaks of a commissural connection between the two 'mittleren lateralen Partien des Riechfeldes.' In their experiments both Poljak and Sunderland demonstrated degenerated fibres in the anterior commissure after a lesion of the temporal cortex, which they regarded as a possible site of origin of the fibres in the posterior limb. After midline lesions in the anterior commissure in the cat, Fox and Schmitz were definitely able to follow degenerated fibres in the posterior limb only to the junction of the commissure with the external capsule. Although in some of their experiments ascending degenerated fibres were observed in the external capsule as well, no conclusions could be drawn about the termination of these fibres. Fox, Fisher and Desalva, after a similar study in the monkey, considered that the major portion of the posterior limb is connected with the middle temporal gyrus, and therefore, that the anterior commissure also contains a neocortical component. In support of their observations, these investigators point out that the topographical relationship between

the anterior commissure and the corpus callosum is approximately the same as that between the middle temporal gyrus and the rest of the neocortex. A contribution of fibres to the anterior commissure from the amygdaloid nucleus has been described by Ban and Omukai (1959) amongst others. With the aid of lesions in different parts of the amygdala, these authors were able to distinguish two groups of fibres: 1) fibres originating from the large-celled anterior portion of the nucleus lateralis and 2) fibres from the large-celled lateral portion of the nucleus basalis and the periamygdaloid cortex. The latter fibres were supposed to reach the commissure via the external capsule. However, like other investigators (Fox; Fox and Schmitz), these authors were unable to demonstrate the existence of an 'interamygdaloid' component of the anterior commissure.

Brodal (1948) studied the origin of the fibres of the anterior commissure by examining retrograde cellular changes after section of the commissure in rats. As the principal sources of these fibres he listed: 'the anterior olfactory nucleus (its dorsal part), the olfactory tubercle, the piriform cortex in its entire extent, the entorhinal area, the bed nucleus of the stria terminalis, the nucleus of the lateral olfactory tract, the medial and cortical and, to some extent, the small-celled part of the basal amygdaloid nuclei, the anterior amygdaloid area and the cortico-amygdaloid transition area, and the neopallial cortex mainly in its posterior and ventral parts.' Electrophysiological methods have also been used in attempts to find the origin and termination of the fibres of the anterior commissure (McCulloch and Garol, 1941; Bailey, Garol and McCulloch, 1941; Garol, 1942). The basic concept of these investigators was that direct interhemispheric connections are formed by the corpus callosum and the anterior commissure, and that the origin and termination of the latter system have a predominantly cortical localization. After strychnine treatment of a large number of areas of one hemisphere, the electrical activity on the other side was charted. In animals with section of the corpus callosum, it was only during stimulation of the pars superior and the pars anterior of the posterior ectosylvian gyrus (area 21) that electric activity could be detected in homologous areas of the contralateral hemisphere. These authors concluded from this that the anterior commissure constitutes a commissural connection between both areas 21.

Until now the introduction of silver impregnation methods into neuroanatomical research has not led to a detailed examination of the posterior limb of the anterior commissure. It is only in the course of other studies that a number of authors have described degeneration of fibres in the posterior limb after lesions of various telencephalic structures. However, exact conclusions

cannot be drawn from these observations either about the origin or about the termination of these fibres. A neocortical origin of the posterior limb was described by Whitlock and Nauta (1956) in Macaca mulatta from the medial and inferior temporal gyrus. They did not find the termination of these commissural fibres. In the opossum, after neocortical and palaeocortical lesions, Way (1966) observed extensive degeneration in both the internal and external capsules. According to him, fibres from the latter system course to the anterior commissure and subsequently spread out in the heterolateral cortex. Knook (1965) concluded from experiments in the rat 'that fibres from extensive cortical regions reach the crus posterius of the anterior commissure either via the corpus callosum and external capsule or directly via the external capsule, but that the majority comes from the piriform cortex. After decussation these fibres terminate partly in the contralateral claustrum but to a greater extent in the adjacent piriform cortex.' Other reports also mention the prepiriform and piriform areas (Sanders-Woudstra, 1961; Powell, Cowan and Raisman, 1963) and the amygdaloid complex (Hall, 1960; Cragg, 1961), as the site of origin of the anterior commissure, while Putnam and Cone (1966) observed termination of fibres from the anterior limb of the anterior commissure in the cortical and medial amygdaloid nuclei. However, in the most recent studies of the afferent and efferent connections of the amygdaloid complex and the adjacent cortex, no reference is made to such a direct relation with the anterior commissure (Nauta and Valenstein, 1958; Nauta, 1961, 1962; Hall, 1963; Cowan, Raisman and Powell, 1965; Powell, Cowan and Raisman, 1965).

The pars ad striam terminalem of the anterior commissure

Although the stria terminalis has several components, all in close relationship with the various areas of the basal telencephalon (Berkelbach van der Sprenkel, 1926), in the present study we shall only discuss the component which contributes to the anterior commissure. This bundle of fibres was first described by Johnston (1923) as a commissural connection between the nuclei of the lateral olfactory tract of both hemispheres. Humphrey (1936), Young (1936) and Miodonski (1966) came to the same conclusion. On the basis of descriptive and experimental anatomical studies, all other investigators stated that the commissural component of the stria terminalis originates from the nucleus of the lateral olfactory tract. There is less agreement in the literature, however, about the termination of these fibres. According to Berkelbach van der Sprenkel (1926) most fibres run to the external capsule after crossing the midline in the anterior commissure, and then terminate in the claustrum. This author believed that only a small portion of the fibres are actually commissural.

Knook (1965) came to the same conclusion, but he mentions also termination in the piriform cortex and possibly in the lateral amygdaloid nucleus. Jeserich (1945) believed that the stria terminalis component of the anterior commissure connects the nuclei of the lateral olfactory tracts of the two hemispheres, and also constitutes an interamygdaloid connection between the medial and cortical amygdaloid nuclei. Lammers and Lohman (1957), and Valverde (1963), have described termination of the stria terminalis component of the anterior commissure in the bed nucleus of the anterior commissure. Finally, some investigators have been unable to trace the fibres of the commissural component of the stria terminalis after their crossing the midline of the brain (Gurdjian, 1925; Fox, 1943; et al., 1943, 1948; Ban and Omukai, 1959; Nauta, 1961).

MATERIAL AND METHODS

This report is based on 47 male New Zealand rabbits (aged 4 months, weighing between 2000 and 2500 g.) in which electrolytic and surgical lesions were placed in the anterior commissure, at various loci in the prepiriform cortex and the neocortex and in a number of subcortical structures of the basal telencephalon. All operations were carried out under Nembutal anaesthesia (30 mg. per kg. body weight intravenously). During the operation anaesthesia was maintained with a mixture of equal volumes of nitrous oxide and oxygen.

The lesions in the anterior commissure and in some of the subcortical cellular areas, were placed stereotaxically with the aid of a modified Dell's apparatus, using Monnier's system of coordinates (1961). Through a burr hole in the skull an electrode with a diameter of 0.3 mm. and insulated but for the terminal 0.5 mm. was introduced. The lesions were made by AC current, the duration of which extended between 15 and 30 seconds. Lesions in the prepiriform cortex and in a few deeper structures of the basal telencephalon were made after enucleation of one eye and removal of the posterior part of the medial wall of the orbit either surgically with a small sharp knife or electrolytically with the insulated electrode described above. Surgical lesions in various parts of the neocortex were placed through trephine openings in the skull.

After survival times varying from 3 to 21 days, the animals were sacrificed. They were perfused transcardially under Nembutal anaesthesia with physiological saline (40 ml. per kg. body weight), followed by 10% formalin (100 ml. per kg. body weight). After at least 6 hours, the brains were removed and

subjected to further fixation in 10% formalin for periods varying between 10 and 30 days. The brains were serially sectioned horizontally, or in some cases transversally on a freezing microtome at 25 μ. In sections stained by the use of the methods of Nauta (1957) and Jacobson (1963), the axonal degeneration of the stem fibres presents itself as rows of black drop-like formations against a light-brown background. Although with these methods valid information can be obtained about the anterograde trajectories of the degenerating axons, they usually fail to disclose the fine-calibered terminal portions of the nerve fibres. Recently, however, the Fink-Heimer method (1967) has offered the opportunity of impregnating not only degenerating nerve fibres but also axon arborizations including synaptic endstructures. These latter phenomena are referred to in the present paper as terminal degeneration.

From preliminary experiments with different postoperative survival times, it appeared that the optimal survival time for degenerating axons of the anterior commissure of the rabbit is 7 days, whereas a survival time of 3 days is optimal for the demonstration of terminal degeneration. For the identification of the various nuclear structures and for the exact localization of the lesions use was made of the combined cell and myelin stain of Klüver and Barrera (1953).

The lesions made can be classified as follows:

1. 18 lesions in or near the anterior commissure (C 1 - C 18). Representative examples of lesions of this category are shown in figs. 1-4.
2. 25 unilateral lesions in various areas of the basal telencephalon and the neocortex (O 1 - O 25, figs. 5-16).
3. 4 unilateral lesions in the stria terminalis (S 1 - S 4, figs. 17-18).

The lesions were charted onto the corresponding atlas drawings of the first part of the present study.

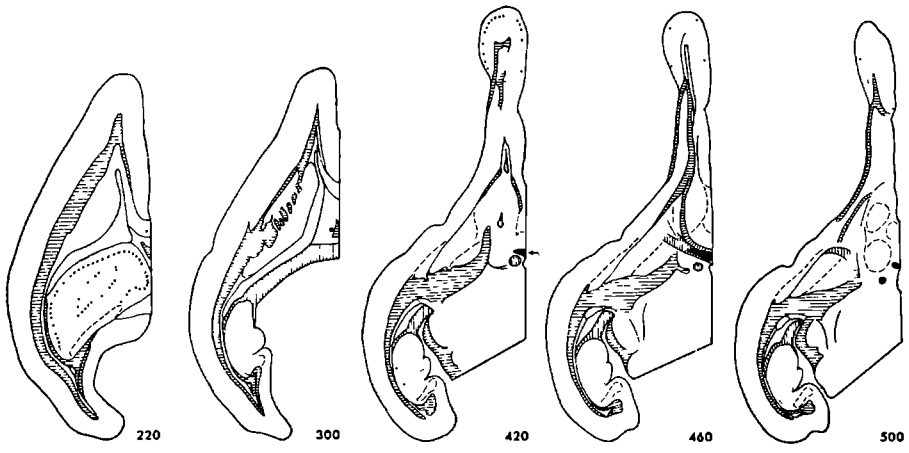


Fig. 1. Rabbit C 1. Lesion in the mid-course of the anterior commissure. Horizontal sections.

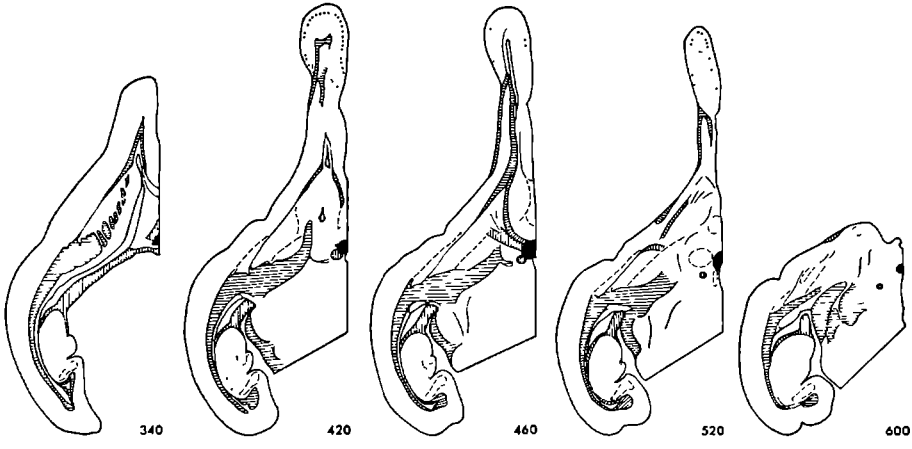


Fig. 2. Rabbit C 2. Lesion in the mid-course of the anterior commissure. Horizontal sections.

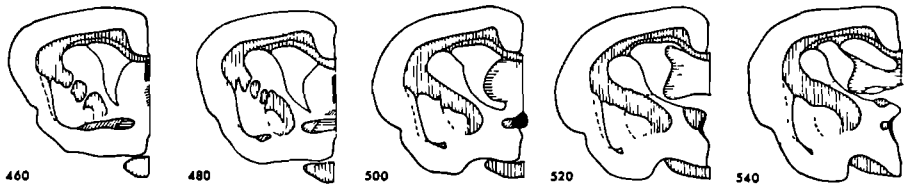


Fig. 3. Rabbit C 9. Lesion in the mid-course of the anterior commissure, Transverse. sections.

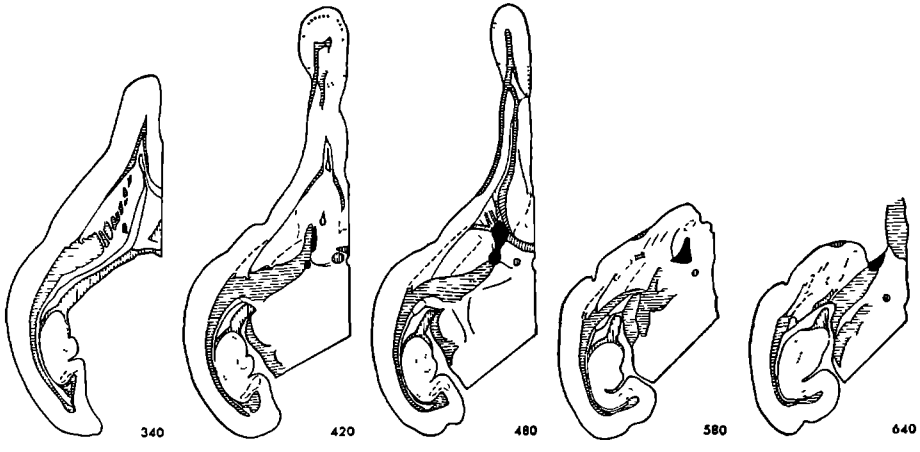


Fig. 3. Rabbit C 9. Lesion in the mid-course of the anterior commissure. Transverse Horizontal sections.

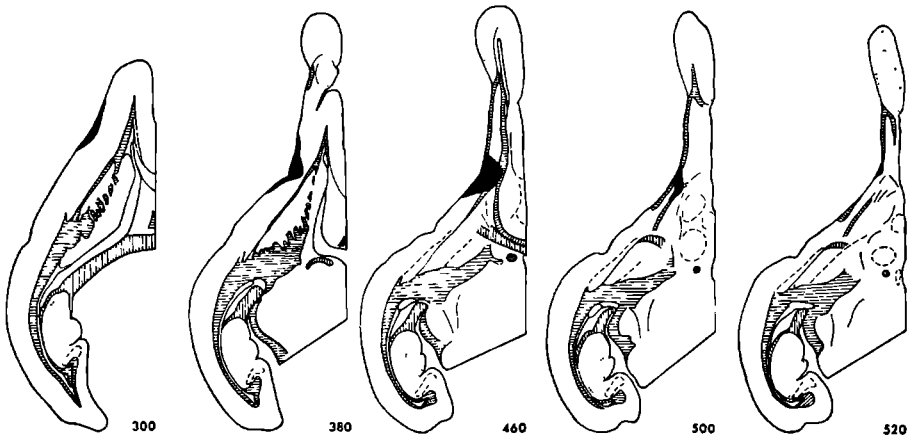


Fig. 5. Rabbit O 1. Lesion in the rostral part of the external capsule and the prepiriform cortex. Horizontal sections.

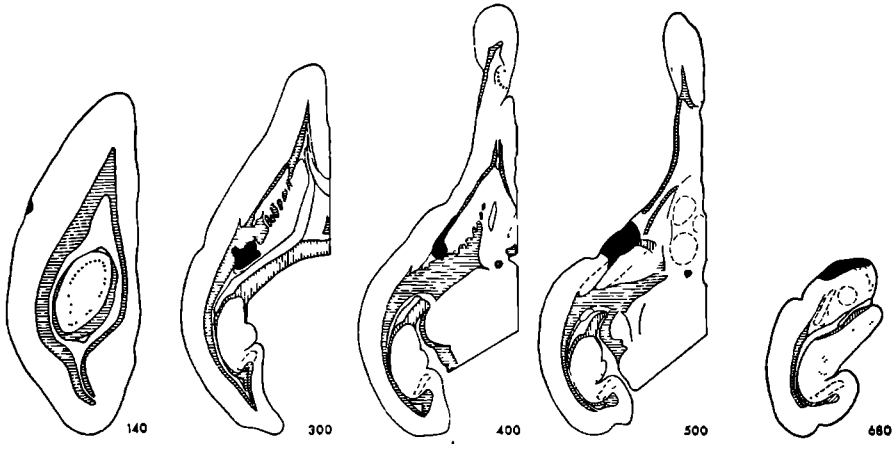


Fig. 6. Rabbit O 5. Lesion in the caudal part of the external capsule and the prepiriform cortex and in the nucleus of the lateral olfactory tract. Horizontal sections.

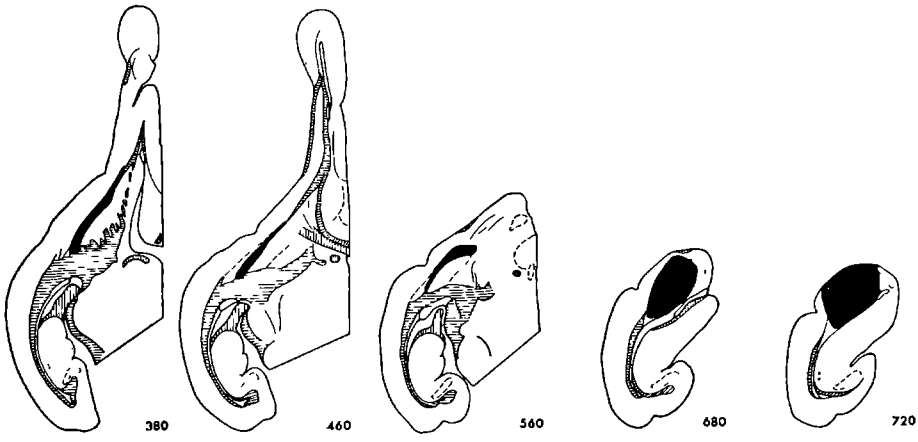


Fig. 7. Rabbit O 9. Lesion in the external capsule and the amygdaloid complex. Horizontal sections.

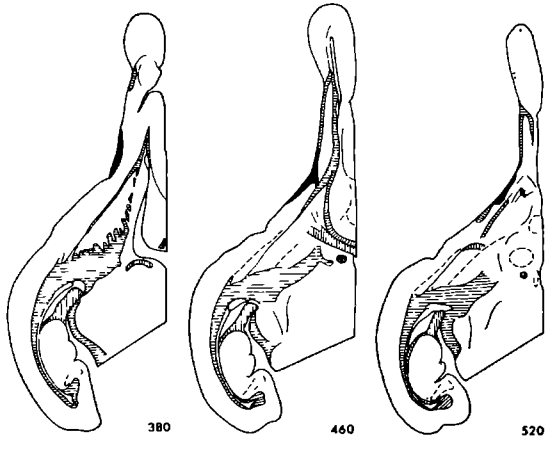


Fig. 8. Rabbit O 11. Lesion in the rostral part of the prepiriform cortex. Horizontal sections.

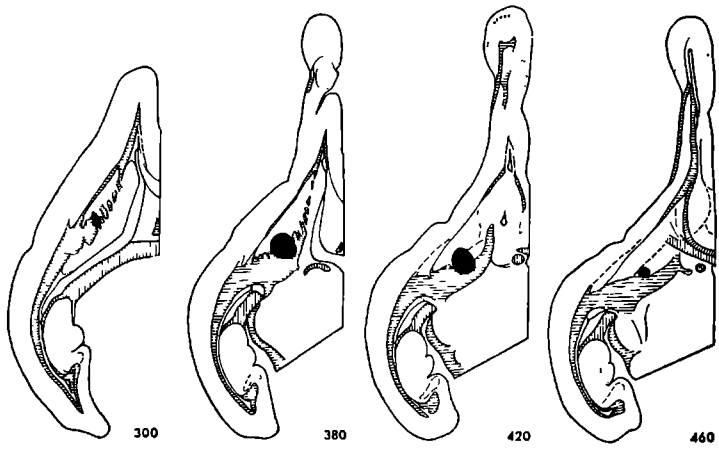


Fig. 9. Rabbit O 12. Lesion in the caudal part of the putamen. Horizontal sections.

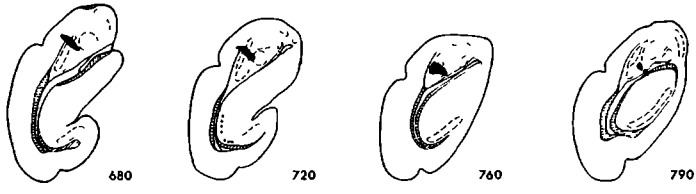


Fig. 10. Rabbit O 14. Lesion in the lateral amygdaloid nucleus. Horizontal sections.

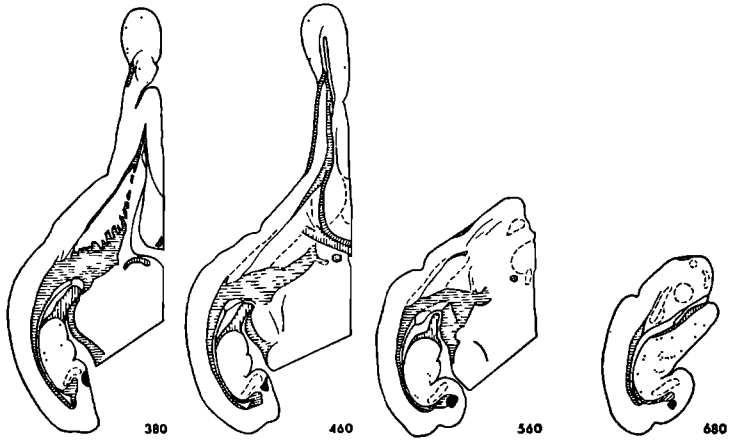


Fig. 11. Rabbit O 15. Lesion in the presubiculum, the parasubiculum and the entorhinal cortex. Horizontal sections.

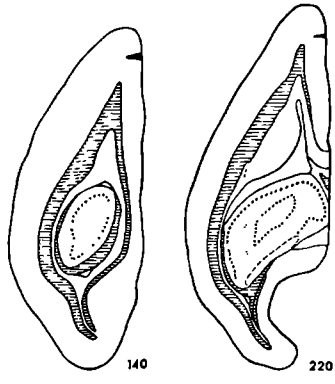


Fig. 12. Rabbit O 17. Lesion in the precentral region of the neocortex. Horizontal sections.

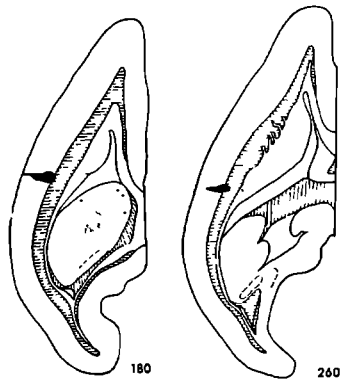


Fig. 13. Rabbit O 19. Lesion in the parietal region of the neocortex. Horizontal sections.

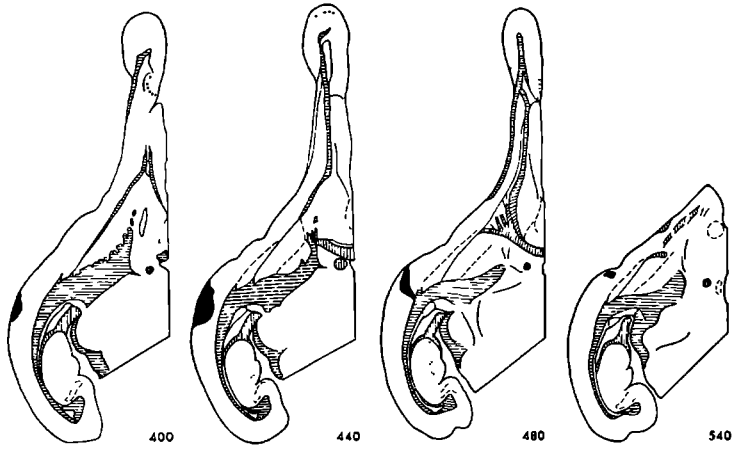


Fig. 14. Rabbit O 20. Lesion in the superior temporal region of the neocortex. Horizontal sections.

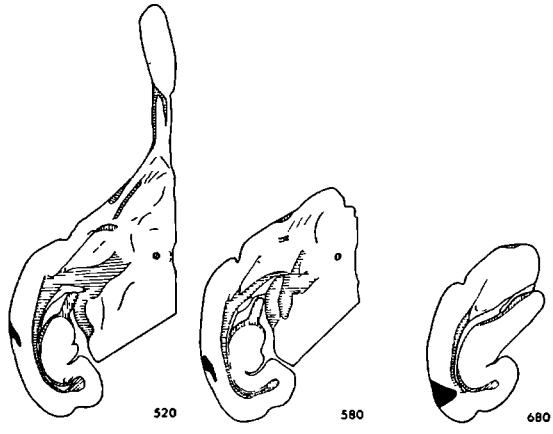


Fig 15 Rabbit O 21 Lesion in the inferior temporal region of the neocortex Horizontal sections.

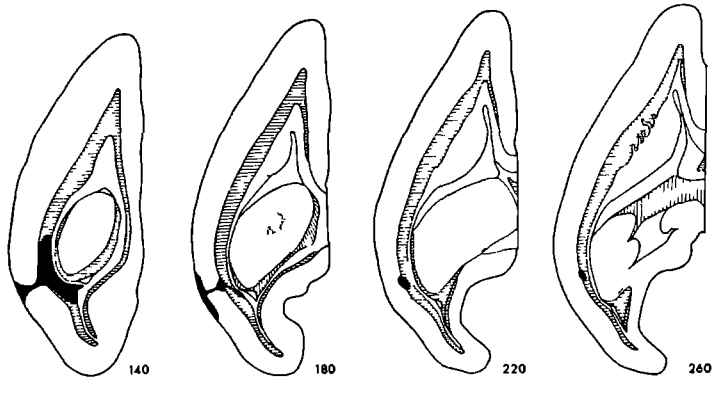


Fig 16 Rabbit O 23 Lesion in the occipital region of the neocortex Horizontal sections

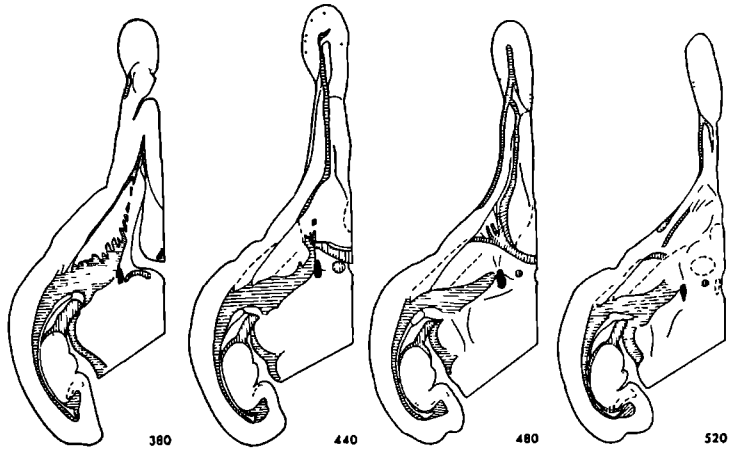


Fig. 17. Rabbit S 1. Lesion in the stria terminalis dorsal to the thalamus. Horizontal sections.

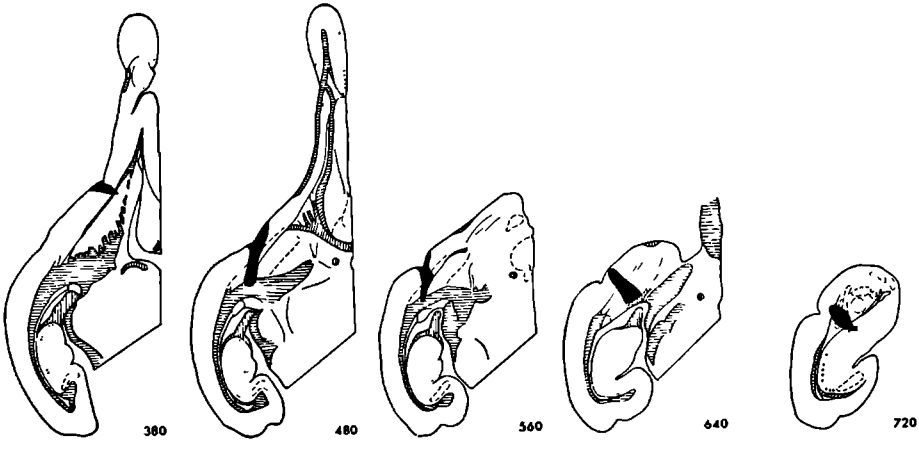


Fig. 18. Rabbit S 3. Lesion in the prepiriform cortex, the amygdaloid complex and the stria terminalis. Horizontal sections.

Lesions in or near the anterior commissure

In 10 rabbits lesions were placed in the anterior commissure in the midline of the brain (series C 1 - C 10). 7 of these brains were sectioned horizontally and 3 in the transverse plane (figs. 1-3). In both hemispheres degenerated fibres can be followed from the lesion in the posterior limb of the anterior commissure. Lateral to the anterior limb of the anterior commissure some of these fibres curve rostralward in the small bundles of the pars transversa of the posterior limb. Although these bundles give off fibres to nuclear masses in the vicinity of the pars transversa (nucleus accumbens and olfactory tubercle), the major portion appears to fan out in the rostral portion of the external capsule. The main bundle of the posterior limb crosses the frontal limb of the internal capsule and gives off degenerated fibres which distribute diffusely to the putamen. The fibres of the main bundle of the posterior limb then curve caudally and fan out in the external capsule, in which they proceed in dorsocaudal and ventrocaudal directions. In the whole vertical extent of the external capsule degenerated fibres can be seen emerging medially and laterally. In the medial direction these fibres penetrate the putamen, while the fibres which emerge laterally pass through the claustrum.

The results of experiment C 11 (fig. 4), in which a unilateral lesion was made in the posterior limb of the anterior commissure, are in accordance with the findings reported above.

In agreement with the observed distribution of the degenerated fibres terminal degeneration was seen by the use of the Fink-Heimer method after a survival time of 3 days in the following areas:

1. The plexiform layer of the entire prepiriform cortex. In the dorsocaudal part of the prepiriform cortex, near the rhinal fissure, a massive termination was observed in the entire plexiform layer with the exception of its most superficial part. In the rostral and ventral parts of the prepiriform cortex the degeneration decreased in intensity and was limited to the deep part of the plexiform layer (fig. 19);
2. The olfactory tubercle. The distribution of terminal degeneration in this area was not only limited to the deep part of the plexiform layer but could also be observed among the cells of the pyramidal cell layer and the polymorph layer (fig. 20);
3. The putamen (fig. 21);
4. The nucleus accumbens;
5. The pars anterior of the lateral amygdaloid nucleus.

No terminal degeneration could be observed in the claustrum, the amygdaloid complex (with the exception of the pars anterior of the lateral amygdaloid nucleus) and the neocortex A distribution of the fibres of the anterior commissure to the bed nucleus of this fibre bundle cannot be stated with certainty because in most animals this nucleus was directly involved in the lesion Only in experiment C 11, where the lesion was situated unilaterally in the anterior commissure, some fibre degeneration could be seen in the area of the bed nucleus on the contralateral side

In most of the series preterminal and terminal degeneration was seen in the anterior portion of the infraradiate region in the medial wall of the hemisphere Although in some cases this degeneration appeared to be in continuity with the degenerated fibres originating from the rostral projection of the external capsule, it cannot be excluded that this phenomenon is due to the penetration of the electrode in the cingulate cortex, or to a lesion of the septum near the anterior commissure

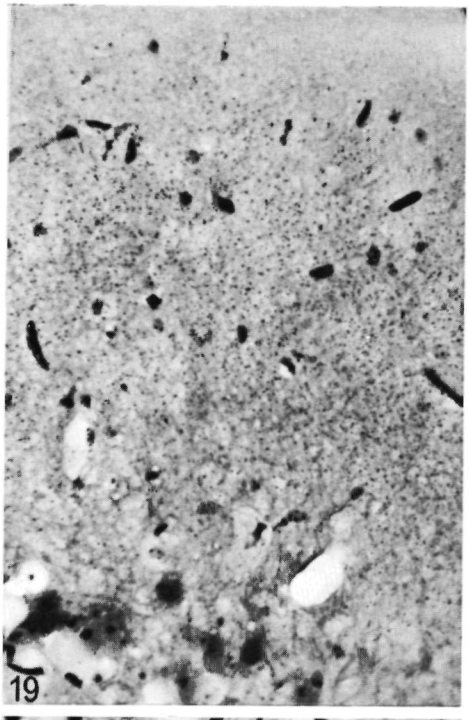
Following midline lesions of the anterior commissure degenerating fibres can also be traced in the commissural component of the stria terminalis These fibres leave the commissure lateral to the column of the fornix and course caudalward together with the other components of the stria terminalis Some of the fibres that constitute the pars ad striam terminalem terminate in the bed nucleus of the stria terminalis With the Fink-Heimer method terminal degeneration is fost apparent laterally in that portion of the nucleus which lies at the level of the anterior commissure However, also in the course of the stria terminalis to the amygdaloid nucleus terminal degeneration occurs between the fibres of this bundle which suggests that the bed nucleus surrounds the stria terminalis throughout its entire trajectory Fig 22 shows the

Fig 19 Terminal degeneration in the plexiform layer of the prepiriform cortex following a midline lesion of the anterior commissure Fink Heimer method 200 ×

Fig 20 Terminal degeneration in the plexiform layer and the pyramidal cell layer of the olfactory tubercle following a midline lesion of the anterior commissure Fink Heimer method 200 ×

Fig 21 Terminal degeneration in the putamen following a midline lesion of the anterior commissure Fink Heimer method 200 ×

Fig 22 Terminal degeneration in the bed nucleus of the stria terminalis dorsal to the thalamus following a midline lesion of the anterior commissure Fink Heimer method 200 ×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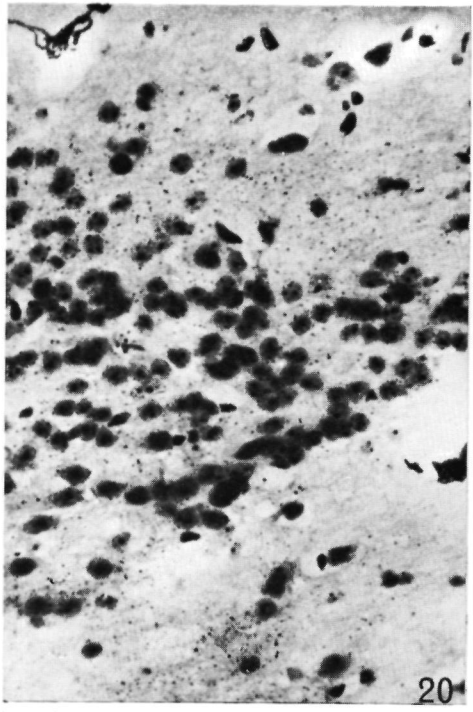
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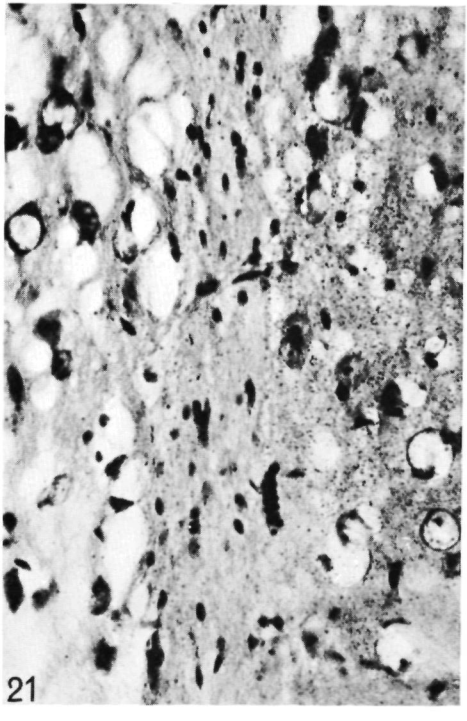
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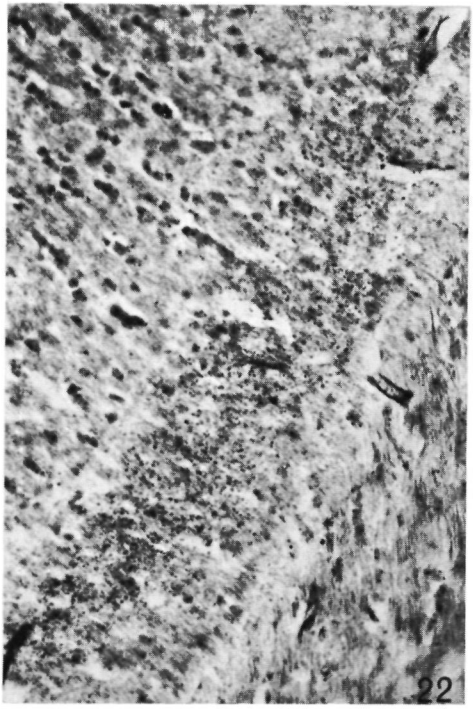
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distribution of the terminal degeneration among the fibres of the stria terminalis in the dorsocaudal part of the bundle. In the ventral course of the stria terminalis, medial to the central amygdaloid nucleus, a fairly compact bundle of degenerated fibres splits off from the rest of the stria terminalis. This bundle passes rostralward through the amygdaloid area and terminates in the nucleus of the lateral olfactory tract. In the latter nucleus terminal degeneration is present superficial to and among the cells of both its lateral and medial parts.

Although in all experiments attempts were made to keep the lesions in the anterior commissure as small as possible, in the majority of the cases they were not confined to the posterior limb and the commissural component of the stria terminalis. Usually the lesions were found to involve adjacent structures, in particular the anterior limb of the anterior commissure, the precommissural and supracommissural portions of the septum, the pre-optic area and the columns of the fornices (see fig. 2). In order to avoid erroneous interpretations lesions were placed in these adjacent areas, without inflicting damage to the posterior limb and the commissural component of the stria terminalis. In 4 rabbits (C 12 - C 15), lesions were placed in the anterior limb of the anterior commissure with only very slight damage to the septum; in 2 cases (C 16 and C 17) lesions were made in the precommissural portion of the septum and in 1 rabbit (C 18) the column of the fornix and the pre-optic area were destroyed unilaterally. In none of these experiments degeneration could be observed in the prepiriform cortex, the olfactory tubercle, the putamen, the nucleus accumbens, the pars anterior of the lateral amygdaloid nucleus and the bed nucleus of the stria terminalis on the contralateral side. This indicates that the bilateral terminal degeneration in these areas after a midline lesion of the anterior commissure is due to fibres of the posterior limb or the pars ad striam terminalem of the anterior commissure. In view of the frequent finding of degeneration in the anterior part of the cingulate cortex following lesions of structures adjacent to the anterior commissure, the question whether this fibre bundle contributes to the infraradiate region still remains open.

Lesions in various parts of the basal telencephalon and neocortex

On the hypothesis that the major portion of the afferent fibres reach the posterior limb of the anterior commissure by way of the external capsule, a number of lesions (O 1 - O 9) were placed in this fibre bundle (for some of these lesions see figs. 5-7). Although it was impossible in these experiments to avoid damage to adjacent areas, such as the prepiriform cortex, the claustrum, the putamen and the nucleus accumbens, it was, however, evident that these

areas do not directly contribute significant numbers of degenerated fibres to the posterior limb of the anterior commissure; almost all the degenerated fibres first join the external capsule and then continue their course in the posterior limb. Fibres from the rostral portion of the external capsule reach the medial portion of the anterior commissure via the pars transversa, whereas fibres from the caudal portion of the external capsule course via the main bundle of the posterior limb. In the midline the fibres of the pars transversa and of the main bundle are completely intermingled.

It could further be demonstrated that, either following lesions of the rostral portion of the external capsule (O 1 - O 4, fig. 5), or of the caudal portion (O 5 - O 8, fig. 6), degenerated fibres of the posterior limb course both rostrally and caudally in the contralateral external capsule. From this observation it can be concluded that the majority of the fibres of the posterior limb are not true commissural fibres connecting identical points on both sides of the midline, but are, in fact, decussating fibres which connect different areas of the two hemispheres.

The terminal degeneration corresponding to the above-mentioned fibre degeneration could a.o. be studied in the experiments O 5 and O 9 (figs. 6 and 7), in which lesions were placed unilaterally in the caudal part of the external capsule. In the contralateral hemisphere degeneration is maximal in the putamen, in the pars anterior of the lateral amygdaloid nucleus and in the prepiriform cortex. In this latter area the distribution of the degenerating terminals is identical to the pattern found following lesions of the anterior commissure (see page 87). On the other hand, in the nucleus accumbens degeneration is only present in its lateral segment alongside the anterior limb of the anterior commissure, whereas degeneration in the olfactory tubercle is completely lacking. These discrepancies with the findings following midline lesions of the anterior commissure may be due to the fact that in the experiments O 5 and O 9 the lesions had caused only slight damage to the rostral portion of the external capsule and the pars transversa.

In cases in which lesions of the external capsule involve the prepiriform cortex (O 1 - O 9) degenerated fibres can be traced from this cortical area into the external capsule. This observation was confirmed in the experiments O 10 and O 11 (fig. 8), where the lesions were confined to the prepiriform cortex without any significant damage to the external capsule. In these latter cases, degenerated fibres, after traversing the claustrum pass into the external capsule and pursue their course in the posterior limb of the anterior commissure. In the contralateral hemisphere the distribution of fibre degeneration is the same as in cases following lesions of the external capsule. Terminal

degeneration can, however, be demonstrated with certainty only in the putamen and in the dorsocaudal part of the prepiriform cortex, probably as a consequence of the small size of the lesions

Not only the prepiriform cortex but also the putamen contributes to the anterior commissure In the experiments O 5 - O 8, where the lesions involve the putamen, degenerated fibres can be traced to the external capsule, whereas some others directly enter the posterior limb of the anterior commissure In order to study the termination of these fibres in the contralateral hemisphere, isolated lesions would have to be made in the putamen without causing damage to the external capsule or the prepiriform cortex This is, however, difficult in view of the fact that the external capsule completely envelopes the putamen Only in one experiment (O 12, fig 9) the lesion was found not to involve the external capsule although in this case the putamen was only partially destroyed Following this lesion terminal degeneration could be demonstrated at the contralateral side in the lateral part of the putamen and in the dorsocaudal portion of the prepiriform cortex

It was not possible to study the claustrum separately as a possible site of origin of commissural fibres, because, as mentioned above, the adjacent external capsule and prepiriform cortex were always involved by lesions in this hourglass shaped nuclear area Moreover, fibres originating from the prepiriform cortex pass through the claustrum before they reach the external capsule, and will be interrupted by lesions in the claustrum It is, however, interesting to note that even in experiments in which the claustrum was damaged (O 5 - O 9), terminal degeneration could not be demonstrated in the contralateral claustrum, thus excluding the existence of a commissural connection between the two claustra

The factors discussed in relation to the putamen and the claustrum also apply to the various amygdaloid nuclei and in particular to the pars anterior of the lateral amygdaloid nucleus From the rostral and lateral sides, the amygdaloid complex can only be approached through the prepiriform cortex and the external capsule, whereas with a dorsal approach the putamen or the posterior limb of the anterior commissure are usually damaged as well (fig 7) In the experiments O 13 and O 14 (fig 10) lesions were made in the amygdaloid complex with negligible damage to adjacent structures Following these small lesions, no distinct contribution to the anterior commissure of fibres could be demonstrated, neither was terminal degeneration seen in the termination areas of the posterior limb, as described above, nor in the contralateral amygdaloid nuclei

In the experiments O 15 (fig 11) and O 16, in which lesions were placed in

the presubiculum, the parasubiculum and the entorhinal cortex, no degenerated fibres were seen in the posterior limb of the anterior commissure.

Finally, in the experiments O 18 - O 25, various areas of the neocortex were damaged, viz.: the precentral region (fig. 12), the parietal region (fig. 13), the superior temporal region (fig. 14), the inferior temporal region (fig. 15) and the occipital region (fig. 16). From all these areas degenerated fibres can be traced into the external capsule. These fibres cross the midline in the posterior limb of the anterior commissure and then fan out rostrally and caudally in the contralateral external capsule. This observation agrees with the findings after section of the anterior commissure in the midline of the brain. In all cases the neocortical contribution of fibres to the posterior limb involved only a small number of fibres, and their precise termination was therefore difficult to determine.

Unilateral lesions in the stria terminalis

In the experiments in which the anterior commissure was interrupted in the midline, the commissural component of the stria terminalis was shown to end in the nucleus of the lateral olfactory tract, and in the bed nucleus of the stria terminalis along the entire course of this fibre bundle (see page 88). For further investigation of this component of the anterior commissure, in the experiments S 1 - S 4 unilateral lesions were made at different sites along the course of the stria terminalis. Two of these lesions are shown in figs. 17 and 18. After section of the stria terminalis dorsal to the thalamus, as well as after damage of the ventral portion of this tract in the amygdaloid complex, degenerated fibres were found running in the stria terminalis from the sites of the lesion toward the anterior commissure. The degenerated fibres of the commissural component of the stria terminalis join the anterior commissure at its dorso-caudal side. After crossing the midline this component continues its course on the contralateral side as described on page 25. By the use of the Fink-Heimer method terminal degeneration was demonstrated contralateral to the lesion both in the bed nucleus of the stria terminalis and in the nucleus of the lateral olfactory tract. These observations were confirmed by the results of experiment O 9 (fig. 7), in which the stria terminalis was damaged in the region of the amygdaloid nucleus.

After interruption of the stria at different sites along its course no differences were found in the density of terminal degeneration in the contralateral bed nucleus of the stria terminalis. On the other hand a difference in density was definitely observable in the contralateral nucleus of the lateral olfactory tract: there was a quite massive degeneration following lesions in the stria terminalis

just dorsocaudal to the anterior commissure, whereas terminal degeneration was much less dense after lesions of this bundle in the amygdaloid complex. Furthermore, in experiment O 5 (fig. 6) in which the entire amygdaloid complex remained undamaged with the exception of the nucleus of the lateral olfactory tract, terminals could be clearly identified in the contralateral bed nucleus of the stria terminalis but not in the contralateral nucleus of the lateral olfactory tract.

From these observations it seems reasonable to conclude that the pars ad striam terminalem of the anterior commissure consists of two components. One component takes its origin from the nucleus of the lateral olfactory tract, runs with the stria terminalis without getting additional input and terminates in the contralateral bed nucleus of the stria terminalis. The other component forms a connection between the bed nucleus of the stria terminalis and the contralateral nucleus of the lateral olfactory tract. Because it continuously receives contributions from the bed nucleus of the stria terminalis as it courses from the amygdaloid complex to the anterior commissure, the composition of this second component is different at different levels.

DISCUSSION

Termination of the posterior limb of the anterior commissure

In the experiments described above it could be demonstrated that the fibres of the posterior limb of the anterior commissure terminate in different areas of the basal telencephalon, viz.: the prepiriform cortex, olfactory tubercle, putamen, nucleus accumbens, pars anterior of the lateral amygdaloid nucleus and, possibly, the bed nucleus of the anterior commissure.

These findings do not agree with the widely held view among older authors according to which the posterior limb of the anterior commissure constitutes a commissural connection between neocortical areas of the two hemispheres (Burdach, 1822; Meynert, 1870, 1872; Ganser, 1879; Young, 1936). However, in the present study termination of fibres of the posterior limb in the neocortex could not be identified. In this connection, it is important to note that, when interpreting the results of anterior commissure lesions, additional damage to the neocortex and the corpus callosum must be minimal. As described, for instance, by Poljak (1927), Ariëns Kappers et al. (1936) and Sunderland (1940) the corpus callosum forms an intercortical connection between the two hemispheres. On their way to the ventrally situated neocortical areas, fibres of the

corpus callosum cross the dorsal portion of the external capsule, may even descend in it over a certain distance and become intermingled with fibres which enter the capsule from the anterior commissure. Because of the mixture of these two kinds of fibres, lesions resulting in fibre degeneration of both the anterior commissure and the corpus callosum give confusing results, e.g., after a partial resection of one hemisphere, as performed, for instance, by Ganser (1879) when studying the anterior commissure, there will also be extensive degeneration in the corpus callosum and in the contralateral neocortex. Sunderland (1940) obtained similar results after much less extensive cortical lesions. This observation may also explain the findings of Fox, Fisher and Desalva (1948) of termination of anterior commissure fibres in the neocortex after a midline lesion in this fibre bundle. These investigators placed electrolytic lesions in the commissure at six different sites 1 mm apart, in order to be certain of complete interruption of this bundle. Because the corpus callosum was penetrated every time by this approach, interruption of a considerable number of callosal fibres is quite possible. In the present study insulated needle electrodes were used, which in the majority of cases caused only very small tracks in the corpus callosum.

An interamygdaloid component of the anterior commissure has been described by Probst (1901), Winkler (1917), Gurdjian (1925), Humphrey (1936) and Ariëns Kappers et al. (1936). Young (1936) held the opinion that only the lateral amygdaloid nuclei of both hemispheres were connected with each other. In the present study termination of the posterior limb was found only in the pars anterior of the lateral amygdaloid nucleus. Degeneration in the lateral amygdaloid nucleus of the rat following a lesion in the contralateral external capsule has also been described by Sanders-Woudstra (1961). In this context it is of interest that like Fox (1943), Fox and Schmitz (1943) and Ban and Omukai (1959), Sanders-Woudstra was unable to demonstrate in her experiments an interamygdaloid component of the anterior commissure.

A connection between the caudal cortical areas of the piriform lobe on both sides of the midline has been reported by Winkler (1917) and Gurdjian (1925). In our material, however, after section of the anterior commissure, no terminal degeneration was seen in the entorhinal cortex, parasubiculum or presubiculum.

In accordance with the observations of most of the above-mentioned investigators the present experiments have demonstrated an extensive distribution of fibres of the anterior commissure to the prepiriform cortex. The terminals of these fibres are not evenly distributed there. In the dorsocaudal part of this cortical area near the rhinal fissure, massive terminal degeneration

was seen in the entire plexiform layer with the exception of its most superficial part In rostral and ventral directions the degeneration decreases in density and is localized exclusively in the deep part of the plexiform layer This difference in the amount and localization of degenerating terminals may perhaps explain the observation of Cajal (1904), who, in Golgi preparations, observed termination of fibres of the anterior commissure only in the most caudal portion of the prepiriform cortex After crossing the midline, fibres to the prepiriform cortex run partly in a rostral direction via the bundles of the pars transversa of the anterior commissure and the anterior portion of the external capsule, whereas the majority of the fibres course in the main bundle of the posterior limb and fan out in the posterior portion of the external capsule After emerging from the external capsule, these fibres pass through the claustrum and have their termination in the prepiriform cortex In the present material stained by the use of the Fink Heimer method no terminal degeneration was found in the claustrum, which is in contradiction to the report of Knook (1965) It appears likely that this investigator in his Nauta Gygax sections interpreted the irregularly arranged degenerating fibres which pass through the claustrum to the prepiriform cortex as preterminal degeneration

In the olfactory tubercle terminal degeneration following section of the anterior commissure can be seen in the plexiform and pyramidal layers and, to a lesser extent, also in the polymorph cell layer Brodal (1948), who studied retrograde cellular changes after lesions in the anterior commissure, already held that 'the occurrence of bilateral changes even when the lesion is unilateral makes probable that at least some of the contributions from this nucleus to the anterior commissure are truly commissural fibres interconnecting the two olfactory tubercles' Fox and Schmitz (1943), in Marchi preparations, were unable to follow fibres from the anterior commissure into the olfactory tubercle However, in view of the gradual decrease of the circumference of the anterior limb of the anterior commissure, they considered a termination of this fibre bundle in the tubercle very likely In our opinion, the fibres ending in the olfactory tubercle are not fibres of the anterior limb but are, in fact, small bundles of the pars transversa which accompany the anterior limb for some distance before distributing to the nucleus accumbens, the olfactory tubercle and the rostral portion of the external capsule

The most important finding of the present experiments is the demonstration of a dense terminal degeneration in the putamen, both following interruption of the anterior commissure in the midline and contralateral lesions of the external capsule Most of the nerve fibres of the commissure reach the putamen via the external capsule, whereas the rostral extension of the putamen,

which is situated ventral to the anterior commissure among the bundles of the pars transversa, receives fibres directly from the main bundle of the posterior limb and from the pars transversa The intimate connection between the putamen and the external capsule lateral to it has already been described by Burdach (1822) and Meynert (1872) However, no data could be found in the literature concerning a connection between the anterior commissure and the putamen In the present study much care has been taken to demonstrate that the terminal degeneration observed in the putamen is due to interruption of anterior commissure fibres and has not been caused by damage to the corpus callosum or telencephalic areas surrounding the anterior commissure Firstly, in experiments in which lesions were placed in the anterior commissure the electrode track in the corpus callosum was in most cases too small to produce such a massive termination in the putamen as was, in fact, seen Secondly, in the experiments C 12 C 18 with lesions in the immediate neighbourhood of the anterior commissure sparing the posterior limb no degeneration in the putamen could be observed Thirdly, in the experiments O 1 O 8, in which lesions were placed unilaterally in the external capsule by basal approach, degeneration was seen in the contralateral putamen

A fibre contribution from the pars transversa of the anterior commissure to the nucleus accumbens, as demonstrated in some of the present experiments, has been described previously only by Gurdjian (1928) in normal material of the rat Knook (1965) failed to demonstrate such a contribution in the rat In the present experiments degeneration in the nucleus accumbens appears much less pronounced than in the putamen, and is mainly confined to the lateral portion of the nucleus situated immediately ventral and medial to the anterior limb of the anterior commissure

Termination of fibres of the anterior commissure in the bed nucleus of this commissure, as previously described by Gurdjian (1925) in the rat, was definitely shown in only one experiment

Origin of the posterior limb of the anterior commissure

In accordance with the myelo architectonic descriptions of the anterior commissure in the rat (Gurdjian, 1925, Kreiner, 1936) and in the rabbit (Young, 1936), it was demonstrated in the present study that the major portion of the afferent fibres reach the posterior limb of the anterior commissure via the external capsule Only a small number of fibres distribute directly to the pars transversa or to the main bundle of the posterior limb The fact that the fibres originating from the various cortical and subcortical areas first course in the external capsule before they contribute to the anterior commissure, is of great

importance for further evaluation of the results of the present experiments As shown by descriptive anatomical studies, there is a very close topographical relation between the external capsule and the cortical and nuclear areas of the basal telencephalon Therefore, lesions in individual areas unavoidably interrupt fibres originating in other areas which run via the external capsule to the anterior commissure Moreover, to avoid excessive damage to adjacent structures, small lesions are essential The number of degenerating fibres resulting from such lesions, however, is often insufficient for tracing them by the use of the Nauta Laidlaw method to their areas of termination on the contralateral hemisphere The more sensitive Fink Heimer method has only recently been developed, and was only used in a small number of our experiments Therefore, in some cases with lesions in restricted areas no information can be given regarding the precise contralateral termination of fibres originating from these areas In these cases, termination of these fibres should be sought in one or more of the areas of termination of the posterior limb mentioned above

Sanders Woudstra (1961) concluded that it is likely that in the rat the posterior limb of the anterior commissure contains not only commissural fibres but also decussating fibres which connect the anterior portion of the prepiriform cortex with the posterior portion of this cortex on the contralateral side On the basis of lesions in different portions of the external capsule, the present experiments have shown that a considerable proportion of the posterior limb fibres, which emerge rostrally and caudally from the external capsule, are decussating fibres which fan out diffusely in the contralateral external capsule These fibres terminate in the entire prepiriform cortex, the putamen, the pars anterior of the lateral amygdaloid nucleus, the nucleus accumbens, and probably also in the olfactory tubercle Furthermore, it was also found that many of the fibres running in the external capsule have their origin in the prepiriform cortex This observation is in agreement with the findings of Brodal (1948), Powell, Cowan and Raisman (1963) and Knook (1965) The conclusion seems therefore justified that the entire prepiriform cortex contributes to a heterotopical projection via the anterior commissure to all the above mentioned areas of termination in the contralateral basal telencephalon, and that there is no topological relationship between different portions of the prepiriform cortex of the two hemispheres

In the present study it was also shown that the entire neocortex diffusely distributes to the posterior limb of the anterior commissure A contribution from the temporal cortex has been described previously by Poljak (1927), Sunderland (1940) and Whitlock and Nauta (1956) Knook (1965) also traced

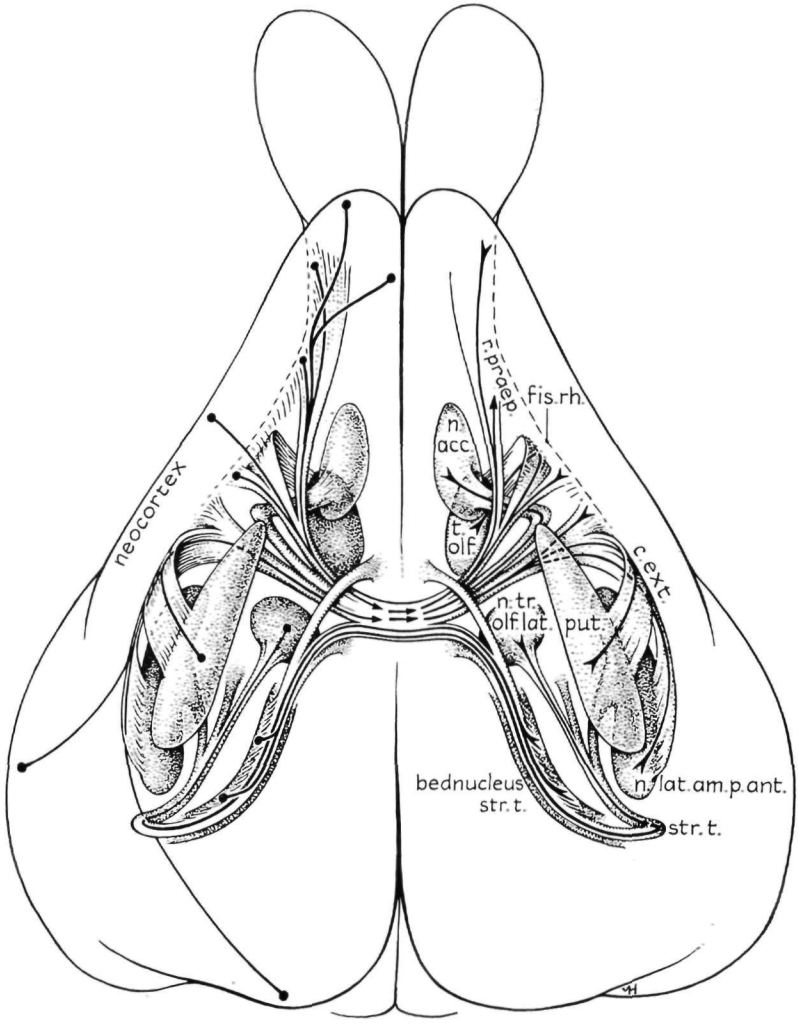

Fig. 23. Diagram of the principal fibre connections via the posterior limb and the stria terminalis component of the anterior commissure.

fibres from other neocortical areas into the anterior commissure. It was not possible in the present material to identify the actual termination of these neocortical fibres on the contralateral side. Since, however, following section of the anterior commissure in the midline of the brain, termination of commissural fibres was not observed in the neocortex by the use of the Fink-Heimer method, a true commissural connection between the two neocortical hemispheres via the anterior commissure must be regarded as highly unlikely. From these data the conclusion can be drawn that there is a diffuse projection from the neocortex to one or more of the terminal areas of the anterior commissure in the contralateral basal telencephalon.

It proved to be difficult to place isolated lesions in the various subcortical areas of the basal telencephalon in order to study the possible origin of commissural fibres from these areas. In making lesions in the claustrum, in the lateral amygdaloid nucleus and in the nucleus accumbens in particular, it was impossible to avoid additional damage to the external capsule and the pars transversa of the anterior commissure. As a result, so many fibres from the neocortex and prepiriform cortex to the anterior commissure were interrupted, that it was not possible to demonstrate with certainty any contribution from the subcortical areas in question. Cowan, Raisman and Powell (1965) engaged similar difficulties in their experiments on amygdaloid connections in the rat. With regard to their findings they stated that 'it is likely that much of what has hitherto been accepted as an amygdalofugal pathway is, in fact, a projection system of fibres from the piriform cortex.' Accordingly, these investigators concluded that there is no major contribution of fibres from the amygdaloid complex to the posterior limb of the anterior commissure, which agrees with the findings of the present experiments. This observation is at variance with the reports of Young (1936), Brodal (1948), Ban and Omukai (1959) and Cragg (1961). Also Gurdjian (1928) stated on the basis of normal rat material that some commissural fibres originate from both the lateral amygdaloid nucleus and the nucleus accumbens, whereas Koikegami, Hirata and Oguma (1967) in an experiment in cats observed degeneration in the anterior commissure after a lesion in the nucleus accumbens.

In two experiments of the present study, in which lesions were largely confined to the putamen, is was possible to trace degenerated fibres to the external capsule, or directly to the posterior limb of the anterior commissure. In one of these cases, with the aid of the Fink-Heimer method, terminal degeneration could be observed on the contralateral side laterally in the putamen and in the dorsocaudal part of the prepiriform cortex. Although, accordingly, part of these fibres form a putamino-putaminal connection, it

seems probable that in the case of the putamen, just as in the case of the neocortex and the prepiriform cortex, the connection is a heterotopical projection to the various contralateral areas of termination of the anterior commissure.

Unlike Brodal (1948), we were unable to show anterior commissure fibres originating from the entorhinal cortex, the parasubiculum or the presubiculum.

In conclusion it might be stated that the present experiments have definitely demonstrated that fibres of the posterior limb of the anterior commissure originate from the prepiriform cortex, the neocortex and the putamen. Although these fibres could not always be followed to their areas of termination it seems, however, highly probable that most of them are not true commissural fibres, but, in fact, constitute a heterotopical connection between the areas of origin and the prepiriform cortex, the putamen, the lateral amygdaloid nucleus, the nucleus accumbens and the olfactory tubercle of the contralateral hemisphere. Origin from other areas than those mentioned above could not be excluded with certainty as the methods used must be regarded as inadequate for solution of this problem. For this purpose, a method will have to be developed which will permit precise identification of retrograde cellular changes after midline lesions in the anterior commissure.

The pars ad striam terminalem of the anterior commissure

From the results of experiments C 1 - C 18, O 5 and S 1 - S 4 the conclusion can be drawn that the pars ad striam terminalem of the anterior commissure (the commissural component of the stria terminalis) consists of two components. One component arises in the nucleus of the lateral olfactory tract, courses with the stria terminalis to the anterior commissure and terminates in the contralateral bed nucleus of the stria terminalis. This latter nucleus is situated along the entire course of the stria terminalis from the anterior commissure to the amygdaloid complex, but has its greatest dimension around the ascending portion of the stria terminalis on the dorsomedial side of the internal capsule.

The second component of the pars ad striam terminalem of the anterior commissure has its origin in the bed nucleus of the stria terminalis, and after crossing the midline, courses together with the other components of the stria terminalis to its termination in the nucleus of the lateral olfactory tract. In this way the pars ad striam terminalem provides a reciprocal connection between the nucleus of the lateral olfactory tract and the contralateral bed nucleus of the stria terminalis and not a commissural connection between the nuclei of the lateral olfactory tract, as has been described by several investigators (John-

ston, 1923, Berkelbach van der Sprenkel, 1926, Gurdjian, 1928, Young, 1936, Jeserich, 1945, Knook, 1965, Miodonski, 1966)

Moreover, Berkelbach van der Sprenkel and Knook have reported termination of the commissural component of the stria terminalis in the claustrum, the piriform cortex and the lateral amygdaloid nucleus It was not possible to confirm these findings in the present experiments, nor was termination of the pars ad striam terminalem observed in the bed nucleus of the anterior commissure (Lammers and Lohman, 1957, Valverde, 1963) It is possible, however, that these terminations were actually localized not in the bed nucleus of the anterior commissure but in that part of the bed nucleus of the stria terminalis which lies at the level of the anterior commissure In all other respects the commissural component of the stria terminalis described by these investigators is identical to the component of the pars ad striam terminalem which originates from the nucleus of the lateral olfactory tract and terminates in the contralateral bed nucleus of the stria terminalis Ban and Omukai (1959) in the rabbit and Heimer and Nauta (1969) in the rat also found evidence of the existence of this component The second component of the pars ad striam terminalem of the anterior commissure which runs in the opposite direction, from the bed nucleus of the stria terminalis to the contralateral nucleus of the lateral olfactory tract has not previously been described

In the first part of the present study a topographical survey is given of the telencephalon of the rabbit, which was used as a basis for the experimental investigations With the aid of serial sections of the brains of adult animals, stained with the method of Kluver Barrera for cells and myelin, an atlas was compiled from drawings and photographs of 16 horizontal sections through the telencephalon, supplemented by drawings of 6 transverse sections

The terminology used for the cortical and subcortical structures is based on the nomenclature of Rose (1931) and Young (1936) A comparative study of the various classifications of the telencephalon now in existence showed to some extent, however, that a number of terms have lost their original meanings and have not always been used in the same way by different authors These terms are considered in detail Subsequently, a topographical classification of the telencephalon of the rabbit is presented, and detailed reference is made to the anatomy and terminology of the piriform region

In the anterior commissure of the rabbit three components can be distinguished the anterior limb, the posterior limb and the pars ad striam terminalem The anterior limb is a compact bundle of fibres which forms a non commissural connection between different parts of the olfactory bulb and the retrobulbar area on both sides of the midline The posterior limb, a term which includes the small laterally and rostrally running bundles of the so called pars transversa, radiates on both sides in the external capsule, before its fibres fan out diffusely The pars ad striam terminalem leaves the anterior commissure immediately after crossing the midline and courses to the amygdaloid complex with the other components of the stria terminalis

The fibre and terminal distribution of the posterior limb and the pars ad striam terminalem of the anterior commissure was studied in adult rabbits with the aid of the Nauta Laidlaw and Fink Heimer methods following electrolytic and surgical lesions The findings obtained in this study can be summarized as follows

1. The posterior limb of the anterior commissure distributes to the prepiriform cortex, putamen, pars anterior of the lateral amygdaloid nucleus, olfactory tubercle, nucleus accumbens and possibly also to the bed nucleus of the anterior commissure.
2. The principal areas of origin of the posterior limb of the anterior commissure are the prepiriform cortex, the entire neocortex and the putamen.
3. Most of the fibres of the posterior limb of the anterior commissure contribute to a decussation rather than to a true commissure.
4. It seems likely that the various areas of origin have a diffuse connection with all the areas of termination of the posterior limb of the anterior commissure on the contralateral side of the cerebrum.
5. The pars ad striam terminalem of the anterior commissure provides a reciprocal connection between the nucleus of the lateral olfactory tract and the contralateral bed nucleus of the stria terminalis.

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Grateful appreciation is expressed to Miss G. Mentink, Mrs. A. Huiskes-Verhoeven, Mr. H. Penso and Mr. P. Spaan for the expert technical assistance. The drawings were made with the co-operation of Mr. Chr. van Huyzen and Mr. E. Noyons. The photographs were made by Mr. A. Reynen.

STELLINGEN

I

De commissura anterior van het konijn is geen echte commissuur.

II

Het is dringend noodzakelijk op korte termijn te komen tot een herziening van de nomenclatuur van het centrale zenuwstelsel.

III

Met de huidige methoden van neuro-anatomisch onderzoek is onvoldoende informatie te verkrijgen omtrent de spino-spinale systemen bij de mens.

IV

De theorie van Prechtl omtrent de phylogenetische betekenis van de grijpreflex bij de menselijke neonatus is onjuist.

K. Poeck: Dtsch. Zschr. f. Nervenhk., 192 (1968), 317.

V

Bij arterio-veneuze fistels van de sinus cavernosus verrichte men een eenmalige definitieve operatie zoals aangegeven door Hamby.

W. B. Hamby: Carotid-cavernous fistula. Springfield (Ill.), 1966.

VI

Ter voorkoming van vroegtijdige sluiting van de bij craniostenose-operaties gemaakte botgroeven verdient het bekleden van de botranden met het buitenblad van de dura mater de voorkeur boven het gebruik van kunststof.

A. J. M. van der Werf: Proefschrift, Amsterdam, 1966.

VII

Over het postoperatieve gebruik van heparine na endarteriectomie bestaat nog steeds geen eenstemmigheid.

F. A. Troost: Proefschrift, Nijmegen, 1968.

VIII

Het is geenszins bewezen, dat periodieke onthouding door overrijpheid van de eicel aanleiding zou geven tot een verhoogde frequentie van congenitale misvormingen bij de mens.

IX

De mening, dat de infantiele spinale spieratrophie steeds een snel progressieve ziekte is met een infauste prognose, is onjuist.

T. L. Munsat, R. Woods, W. Fowler and C. Pearson: Brain, 92 (1969), 9.

X

Indien de opvangorganisatie van 'spoedeisende gevallen', aangegeven door de tweede commissie traumatologie, uitvoerbaar wordt geacht, dan is spoedige realisatie hiervan ook aangewezen.

Nijmegen, 23 juni 1969 H. A. M. VAN ALPHEN